

A.D. Buijse

**DYNAMICS AND EXPLOITATION OF
UNSTABLE PERCID POPULATIONS**



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Dr. N. Daan, buitengewoon hoogleraar
Hydrobiologie.

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Trefw.: visserij ; onderzoek.

1. Gezien de voedselbeschikbaarheid in het IJsselmeer voor eenzomerige snoekbaars zal een beheersmaatregel, die een vergroting van de thans zeer geringe paaistand tot gevolg heeft, direct leiden tot een verhoging van de oogst.
2. Het overschakelen op het eten van vis bij eenzomerige snoekbaars in het IJsselmeer is cruciaal voor de overleving.
3. De stabiliteit in de oogst van baars ten opzichte van die van snoekbaars wordt veroorzaakt door compensatoire mortaliteit.
4. In de visserij moet variatie in de oogst als een gevolg van variatie in aanwas als een fait accompli beschouwd worden.
5. De omvang van de beschikbare gegevensbestanden voor dit proefschrift wijst erop dat analyses reeds in een eerder stadium hadden moeten plaatsvinden.
6. De conclusie van Loftus: "Politicians are constrained in their effort to implement the long-range programs required in resource management, because they face short election cycles." is ook van toepassing op de Nederlandse situatie.
K. H. Loftus. 1987. Inadequate science transfer: an issue to effective fisheries management. Trans. Am. Fish. Soc. 116: 314-319
7. Bij overbevissing moet het verwijtende vingertje niet naar de vissers maar naar de beheerder uitgestoken worden.
8. De aaibaarheidsfactor van het individu maakt discussies over de exploitatie van de populatie irrationeel.
9. Het Rijn Actie Plan leidt meer tot het paaien van mensen dan tot het paaien van zalmen.
10. Koolzuur en fosfaten belemmeren schaatsenrijders in hun voortbeweging.
11. Het fungeren als lijdend voorwerp in deze studie was iets onbenijdbaaars.
12. De geringe aandacht van de politiek voor gokverslaving komt omdat de hiermee behepte personen een melkkoe zijn voor de staatskas.
13. Het abrupt afzeggen van werkafspraken tijdens perioden met natuurijs is een geaccepteerde nationale afwijking.
14. In troebel water is 't goed vissen.

Stellingen behorend bij het proefschrift van A.D.Buijse:
"Dynamics and exploitation of unstable percid populations".

Wageningen, 13 mei 1992.

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Curriculum vitae

Voor mijn ouders

This thesis has been accomplished at
the Department of Fish Culture and Fisheries
of the Agricultural University, Wageningen, The Netherlands

DANKWOORD

Ik zou geen moment willen suggereren, dat het maken van dit proefschrift een one-man show is geweest. Daarom eerst dit dankwoord.

Mijn keuze om in 1987 de functie als AIO te accepteren werd mede bepaald door het vertrouwen in mijn directe begeleider, Wim van Densen. Met name in het eerste jaar heb ik kunnen blindvaren op zijn ervaring met veldwerk en gedurende de hele periode op zijn inzichten in het uitgebreide aanbod van literatuur van de baarsachtigen en zijn "helicopter view" om werkzaamheden te overzien.

Wetenschappelijk onderzoek heeft een zeker oneindig karakter, terwijl een AIO zich hoort te beperken tot de vier jaar waarbinnen de werkzaamheden worden afgerond. Naast wetenschappelijke begeleiding heeft mijn promotor Bram Huisman mij daar dikwijls op gewezen, wat geresulteerd heeft in het feit dat dit proefschrift nu voor u ligt.

De bereidheid van Niels Daan, najaar 1990, als tweede promotor op te treden was een signaal dat ik op de goede weg was. Zijn gestructureerde kritiek op de manuscripten heeft tot wezenlijke verbeteringen geleid.

Anderhalf jaar op dezelfde kamer en dan 's avonds nog een relativerend biertje pakken in de Vlaamse Reus. Joost Backx weet als geen ander hoe het onderzoek de afgelopen jaren verlopen is. Zijn vriendschap en samenwerking zijn mij veel waard.

Net zoals andere vakgroepmedewerkers en studenten heb ik dankbaar gebruik gemaakt van de computerkennis van Marcel Machiels. Zijn overgang van visteelt naar visserij beschouw ik als een waardevolle aanwinst voor onze "sectie".

Studenten zijn de waterdragers van het wetenschappelijk onderzoek. In 1987 bestond de groep uit Alvean Fentener van Vlissingen, Jos Pet, Tim Vriese en Pieter Winkelmolen; in 1988 uit Sophie Brasseur, Rob Houthuijzen, Marcel Klinge en Ronald Lanthers; in 1989 uit Bram Born, Tammo Bult, René Remmerswaal en Wim van Zuilekom en in 1990 volledig uit Siebold van Breukelen. Deze groep stimuleerde mij om er vier jaar enthousiast mee door te gaan. Het werk van sommigen heb ik reeds kunnen vervatten in wetenschappelijke publikaties. Voor anderen zal ik mij in de toekomst nog inzetten.

Samen met Ad van der Sluiszen was het mogelijk om al na korte tijd routinematig monstertochten op het IJsselmeer uit te voeren. Er is letterlijk niets in het water gevallen.

Ik ben verheugd, dat de samenwerking met de zoetwaterafdeling van het Rijksinstituut voor Visserijonderzoek gedurende het project steeds beter is gaan verlopen. Ik vond bij Willem Dekker en Leo Schaap altijd de bereidheid om mij met mijn onderzoek te helpen.

Henk Oudelaar heeft er zorg voor gedragen, dat er sinds 1966 proefvisserijen op het IJsselmeer zijn uitgevoerd. Het bestaan van deze gegevensbestanden vormt een van de belangrijkste poten onder mijn proefschrift.

Ik heb veel met de computer geprutst om een fatsoenlijk kaartje van het IJsselmeer te produceren. Het handwerk van Karel Boekhorst leidde echter tot betere resultaten.

Uitwisseling van gedachten met de andere medewerkers van de vakgroep Visteelt en Visserij vond meestal plaats boven een kop koffie: constructief en lekker luchtig.

Ik ben altijd met plezier gaan monsteren op het IJsselmeer, wat mede te danken is aan het vakmanschap van en de samenwerking met de bemanning van de "Stern": Cees de Rooy, Sjaak Timmermans, Ab Bregman en Joop Markenstein.

Het LEB-fonds en het Produktschap voor Vis en Visprodukten hebben financieel bijgedragen aan de totstandkoming van dit proefschrift. Jaap van der Peyl was bereid dit proefschrift zonder zakelijke onderhandelingen grafisch vorm te geven.

Er is leven naast de promotie. Een "rondje Posbank" met de fiets op een zwoele zomeravond of lekker bochtjes lopen op de Vechtse Banen doen je een werkdag vergeten. De gezelligheid en positieve competitie van de "Schaats Trainingsgroep Wageningen" wordt dan ook zeer gewaardeerd. Het werk en het leven mag ik ook graag boven een of ander glas Belgisch bier evalueren. Gelukkig hoef ik dat nooit alleen te doen en vind bij mijn huisgenoten, Bert en Siebold, bijna altijd een droge keel en een gewillig oor voor een goed gesprek.

Daarnaast zijn er nog vele personen die anoniem wilden blijven. Zij weten dat ik hun steun en vriendschap op grote prijs stel.

SUMMARY

The gill net fishery on perch (*Perca fluviatilis*) and especially the highly valued pikeperch (*Stizostedion lucioperca*) in Lake IJssel is characterised by large variations in the yield. These variations are caused by variations in year-class strength in combination with the high exploitation rate. In the present study a start has been made to explain the causes for variations in year-class strength. In addition, possible management measures are evaluated for their effectiveness in optimising yield. The possibilities for yield optimisation depend on the dynamics of the stocks. Dynamics are determined by recruitment, growth and mortality. The development in the stocks and the fishery has been documented in the past to some extent. Surveys have been conducted since 1966, mainly using a bottom trawl. However, the information obtained through these surveys on the fish stocks had hardly been analysed until now. The present study comprises analyses of these historical trawl surveys on the one hand and of detailed field observations conducted from 1987-1989 on the other. Results were used as input for a size- and age-structured simulation model. This model is developed to evaluate the effectiveness of various management measures to enlarge and stabilise the yield.

Bottom trawl surveys are carried out every autumn to estimate the relative abundance of six major fish species, with particular reference to pikeperch and perch. It is generally supposed among fishermen that the catchability of these species is influenced by light intensity at the bottom, which in this study was characterised by water depth and water clarity as measured by a Secchi-disk. In autumn, water clarity may change greatly from day to day because of wind-mediated re-suspension of sediments. Catchability of ruffe (*Gymnocephalus cernua*) and age 0 pikeperch showed a significant inverse relationship with light intensity at the bottom and, therefore, a correction should be made when catch data for these species are used to estimate population size or year-class strength. Results were not consistent for perch, while for smelt (*Osmerus eperlanus*), roach (*Rutilus rutilus*) and bream (*Abramis brama*) the influence of light intensity upon catchability was not significant. Corrected and uncorrected estimates of the abundance of age 0 pikeperch, based on trawl samples, were compared to demonstrate the effect of water clarity. The correction was marginal for the historical trawl surveys, because sampling was mainly done when conditions were good. Increased water clarity by net avoidance behaviour may lead to zero catches and consequently diminish the effectiveness of sampling programmes. Based on the present analysis, surveys can be optimised by interrupting them when zero catches are likely to occur. For the assessment of age 0 pikeperch abundance, surveys should be interrupted when the ratio between water depth and water clarity is smaller than eight.

Recruitment, indexed as the age 0 abundance in bottom trawls, of perch varied 400-fold and of pikeperch 70-fold over the period 1966-89. Year-class strength variation of perch in Lake IJssel was higher than observed in *Perca* spp. in other waters according to the literature, while for pikeperch it fell within the observed range of *Stizostedion* spp.. Hypotheses were formulated on the possible relationship between recruitment and stock biomass, prey fish availability, water temperature and wind velocity. For perch 36% to 71% of the variation in recruitment could be explained by stock biomass of piscivorous fish, water temperature, and year of sampling; for pikeperch 38% to 86% could be explained by water temperature, wind velocity and year of sampling. For both species strong year-classes were favoured by low temperatures in April and by high summer temperatures; a late increase in water temperature to above 8°C and a high warming rate thereafter, probably resulting in postponed spawning and rapid development, favoured recruitment of perch. Stock-recruitment relationships could not be demonstrated. The impact of the commercial fishery, which possibly accounted for the significant correlation between year of sampling and year-class strength, and of fish-eating birds might have clouded interactions among fish species. Based on this analysis, it is concluded that recruitment will be very difficult if not impossible to manage.

The positive effect of warm summers on recruitment of age 0 pikeperch is most probably caused by its faster growth at higher temperatures than that of its potential prey, age 0 smelt. Mean length of age 0 pikeperch in November correlated strongly with mean summer temperature. Depending on the environmental conditions (especially water temperature and availability of food) the unimodal length frequency distribution of age 0 pikeperch developed into a positively skewed, bimodal or negatively skewed distribution towards the end of the summer. Strong year-classes were characterised by larger mean lengths, and a negatively skewed frequency distribution, while weak year-classes were smaller and positively skewed. Body energy content increased with fish length and differences in body constituents were more pronounced later in the season. The condition of non-piscivorous age 0 pikeperch was low and decreased over time, while that of piscivorous pikeperch increased over time. The onset of piscivory, favoured by high temperatures during summer, has a direct positive effect on the growth and survival of age 0 pikeperch.

Also for perch the onset of piscivory has a positive effect on growth. Growth and size distributions of perch were studied in relation to prey choice and water temperature. Growth of age 0 perch is density-dependent and positively influenced by high summer temperatures. Between 10 and 20 cm perch switched from a diet of zooplankton and macrofauna (*Neomysis integer* and *Gammarus* spp.) towards fish. Age 0 European smelt was the main fish prey. The onset of piscivory occurred at a larger length when mean length of

daphnids was large or when age 0 smelt densities were low. Growth was faster for piscivores than for non-piscivores. Consequently, size distributions of cohorts of which only the larger ones were piscivorous became positively skewed, and initial growth differences between males and females were enhanced. Besides age 0 smelt, perch also fed on age 1 smelt, age 0 perch and age 0 ruffe, but Ivlev indices revealed a preference for age 0 smelt. Cannibalism by older age-groups was rare when recruitment was low, but became common when age 0 densities of perch were high. It is concluded that smelt plays a key role in the population dynamics of both pikeperch and perch, because it facilitates the onset of piscivory thereby enhancing growth and in case of pikeperch also survival. Moreover it buffers cannibalism.

A size- and age-structured simulation model is presented for evaluation of management measures for multispecies gill net fisheries. Data on the dynamics and exploitation of pikeperch and perch were used as parameters for the model. The model takes size distributions within age-groups into account. In the model, growth is determined by length and temperature and dispersion in size distributions is controlled by the 'fractional boxcar train' method. The model is applied to evaluate the integrated short-term and long-term effects of management measures such as mesh size regulations, fishing effort limitations and combinations of both on the biomass, the size and age structure of the stock and of the yield. Changes in yield during the transitional period after a management measure has been implemented, can be quantified.

Finally a simple method is used, which relates the variation in the yield to the variation in recruitment and the exploitation pattern per species. This model neglects stock-recruitment relationships and other density-dependent processes, i.e. the model takes variations in year-class strength for granted and evaluates its consequences for management. It is shown that in case of the Lake IJssel gill net fishery a larger number of age-groups in the catch reduces the inter-annual variation in the yield caused by variable recruitment only to a small extent. Based on their age 0 abundance during the autumn trawl surveys the yield of that year-class can be predicted. For perch the upper and lower 95% confidence limits around this prediction differ by a factor 1.6 and for pikeperch by a factor 2.7. As a consequence of the large variations in year-class strength and the uncertainties in yield prediction, it will be almost impossible to demonstrate the effect of altered management, if the increase in yield merely comprises a higher yield per recruit. Perhaps the largest gain in yield for the gill net fishery is achieved by enlarging the spawning stock biomass of pikeperch especially. More extreme measurements like e.g. temporarily closing the fishery at the southern part of Lake IJssel, might provide the insights for this.

SAMENVATTING

In het IJsselmeer wordt de kieuwnetvisserij op baars (*Perca fluviatilis*) en vooral die op de waardevolle snoekbaars (*Stizostedion lucioperca*) gekarakteriseerd door grote variaties in de oogst. Deze variaties worden veroorzaakt door variaties in jaarklassterkte en door een hoge exploitatiedruk. In deze studie is getracht een verklaring te vinden voor de variaties in jaarklassterkte. Daarnaast is geëvalueerd hoe de visserij beheerd zou moeten worden om de oogst te optimaliseren. De mogelijkheden tot oogstopimalisatie zijn afhankelijk van de dynamiek van de visbestanden. De dynamiek wordt bepaald door recrutering, groei en sterfte. De ontwikkeling in de visstand en de visserij zijn in de loop der tijd ten dele gedocumenteerd. Zo zijn er sinds 1966 proefvisserijen op het IJsselmeer uitgevoerd. Dit gebeurde hoofdzakelijk met een grote aalkuil. De informatie over de visstand, die in deze gegevens opgeslagen ligt, was tot op heden onderbenut. De huidige studie bestaat uit een analyse van deze historische kuilbemonsteringen enerzijds en van gedetailleerde veldwaarnemingen gedurende de periode 1987-1989 anderzijds. De resultaten zijn gebruikt als invoergegevens voor een lengte- en leeftijd-gestructureerd simulatiemodel. Dit model is ontwikkeld om de mogelijkheden tot verhoging en stabilisering van de oogst van een kieuwnetvisserij op basis van diverse beheersscenario's te evalueren.

Kuilbemonsteringen zijn ieder najaar uitgevoerd om de relatieve abundantie van zes belangrijke vissoorten, vooral die van snoekbaars en baars, te schatten. Het algemene idee, dat bij de beroepsvissers leeft, is dat de vangbaarheid van deze soorten wordt beïnvloed door de lichtintensiteit bij de bodem, dat hier gekarakteriseerd is als de verhouding tussen de totale diepte en de zichtdiepte van het water, welke laatste gemeten is met een Secchi-schijf. In het najaar kan de helderheid van dag tot dag sterk variëren als gevolg van het door de wind opgewerveld bodemmateriaal. De vangbaarheid van pos (*Gymnocephalus cernua*) en 0+ snoekbaars daalde bij een toenemende lichtintensiteit bij de bodem. Daarom zouden vangstgegevens van deze soorten gecorrigeerd moeten worden als ze gebruikt worden om bestandsomvang en jaarklassterkte te schatten. De resultaten waren niet eenduidig voor baars, terwijl voor spiering (*Osmerus eperlanus*), blankvoorn (*Rutilus rutilus*) en brasem (*Abramis brama*) geen significant effect van het lichtintensiteit op de vangbaarheid kon worden aangetoond. Voor lichtintensiteit gecorrigeerde en ongecorrigeerde schattingen van dichtheden van 0+ snoekbaars zijn met elkaar vergeleken om het effect van de helderheid van het water te demonstreren. De consequenties voor de historische gegevens bleken gering, omdat bemonsteringsprogramma's hoofdzakelijk uitgevoerd zijn bij goede vangstomstandigheden (troebel water). Een grotere helderheid van het water kan door netontwijkingsgedrag leiden tot

'nul'-vangsten, die de effectiviteit van monsterprogramma's verminderen. De huidige analyse biedt de mogelijkheid om bemonsteringsprogramma's te optimaliseren door ze te onderbreken indien de vangstomstandigheden doen veronderstellen dat de kans op 'nul'-vangsten groot wordt. Voor schattingen van de dichtheden van 0+ snoekbaars betekent dit dat de bemonstering onderbroken zou moeten worden als de verhouding tussen de totale diepte en de zichtdiepte van het water minder dan 8 bedraagt.

De jaarklassterkte (recrutering) wordt in het IJsselmeer geïndexeerd als het aantal 0+ vissen per standaard kuiltrek tijdens najaarsbemonsteringen. Voor baars varieerde de jaarklassterkte met een factor 400 en voor snoekbaars met een factor 70 over de periode 1966-1989. De jaarklassterktevariatie van baars in het IJsselmeer was sterker dan elders beschreven voor *Perca* spp., terwijl die van snoekbaars binnen de elders waargenomen variatie in jaarklassterkte van *Stizostedion* spp. viel. Er zijn hypothesen geformuleerd over de mogelijke relaties tussen recrutering enerzijds en bestandsomvang, beschikbaarheid aan prooivis, watertemperatuur en windsnelheid anderzijds. Voor baars kon 36% tot 71% van de variatie in recrutering verklaard worden door variaties in het bestand aan visetende roofvis, in de watertemperatuur en door het jaar van bemonstering. Voor snoekbaars kon 38% tot 76% verklaard worden door de watertemperatuur, de windsnelheid en het jaar van bemonstering. Sterke jaarklassen ontstonden voor beide soorten in jaren met lage temperaturen in april en in jaren met hoge zomertemperaturen. De met de lage temperatuur in april samenhangende late stijging van de watertemperatuur tot boven de 8°C en de snelle temperatuurstijging daarna, waarschijnlijk resulterend in een uitgestelde paai en een snelle ontwikkeling, had een positief effect op de recrutering van baars. Een relatie tussen de omvang van het bestand en de recrutering kon niet worden aangetoond. De toenemende invloed van de commerciële aalvisserij, die mogelijk de oorzaak is voor de relatie tussen het jaar van bemonstering en de jaarklassterkte, en van de visetende vogels zouden de interacties tussen de vissoorten beïnvloed kunnen hebben. Op grond van deze analyse lijkt de recrutering moeilijk en zo mogelijk niet beheersbaar te zijn.

Het positieve effect van warme zomers op de recrutering van 0+ snoekbaars wordt waarschijnlijk verklaard doordat de 0+ snoekbaars bij hogere temperaturen sneller groeit dan zijn potentiële prooi, 0+ spiering. De gemiddelde lengte van 0+ snoekbaars in november correleerde sterk met de gemiddelde zomertemperatuur. Afhankelijk van de omgevingscondities (vooral watertemperatuur en voedselbeschikbaarheid) ontwikkelden in de zomer nog eentoppige lengtefrequentieverdelingen van 0+ snoekbaars zich tegen het eind van de zomer in rechts-scheve, tweetoppige of links-scheve verdelingen. Sterke jaarklassen worden gekarakteriseerd door een grotere gemiddelde lengte en een links-scheve verdeling, en zwakke jaarklassen door een kleinere gemiddelde

lengte en een rechts-scheve verdeling. De energieinhoud per gewichtseenheid van 0+ snoekbaars nam toe met de lengte en dit verschil werd later in het seizoen sterker. De conditie van de kleinere 0+ snoekbaars, die geen vis at, was laag en nam af door de loop van de tijd, terwijl die van de grotere visetende 0+ snoekbaars juist toenam. De overgang naar het eten van vis, bevordert door hoge zomertemperaturen, heeft een direct positief effect op de groei en overleving van 0+ snoekbaars.

Ook voor baars heeft de overgang naar het eten van vis een positief effect op de groei. De groei en grootteverdelingen van baars zijn onderzocht in relatie tot voedselkeuze en watertemperatuur. De groei van 0+ baars is dichtheidsafhankelijk en wordt positief beïnvloed door hoge zomertemperaturen. Tussen 10 en 20 cm schakelt baars over van een dieet bestaande uit zooplankton en macrofauna (aasgarnaal *Neomysis integer* en vlokreeft *Gammarus* spp.) op het eten van vis. 0+ Spiering was de belangrijkste prooivis. De overgang vond bij een grotere lengte plaats als de gemiddelde lengte van watervlooien (*Daphnia* spp.) groot was of de dichtheden van 0+ spiering laag. Indien alleen de grootste vissen viseter waren resulteerde dit in het links-scheef worden van grootteverdelingen en in het versterken van groeiverschillen tussen mannetjes en vrouwtjes. Baars at naast 0+ spiering ook 1+ spiering, 0+ baars en 0+ pos. Kannibalisme door oudere leeftijdsgroepen was zeldzaam wanneer de dichtheden van 0+ baars laag waren, maar was algemeen bij hoge dichtheden. Geconcludeerd kan worden, dat spiering een sleutelrol speelt in de populatiedynamiek van snoekbaars en baars, omdat het de overgang naar het eten van vis vergemakkelijkt en daarbij de groei en in het geval van snoekbaars ook de overleving bevordert. Bovendien buffert spiering het kannibalisme.

Er is een grootte- en leeftijd-gestructureerd simulatiemodel ontwikkeld ten behoeve van de evaluatie van beheersscenario's voor kieuwnetvisserijen. Gegevens over de dynamiek en exploitatie van snoekbaars en baars in het IJsselmeer zijn gebruikt als parameters voor het model. Het model houdt rekening met de grootteverdelingen binnen leeftijdsgroepen. In het model wordt de groei bepaald door de lichaamslengte en de watertemperatuur. De spreiding in grootteverdelingen wordt gestuurd door de 'fractional boxcar train' methode. Het model is toegepast om zowel korte- als lange-termijn effecten van beheersmaatregelen zoals maaswijdtevoorschriften, beperking van de visserijinspanning of een combinatie van beide op de omvang, de grootte- en leeftijdsstructuur van de visstand en de oogst te evalueren. Ook veranderingen in de oogst tijdens de overgangsperiode na het implementeren van een beheersmaatregel kunnen worden geëvalueerd.

Tenslotte is een eenvoudig model gebruikt, dat de variatie in de totale oogst relateert aan de variatie in recrutering. Het model negeert mogelijke interacties tussen bestand en recrutering en andere dichtheidsafhankelijke processen. Met

andere woorden variaties in jaarklassterkte worden opgevat als een fait accompli. Het model laat zien dat voor de kieuwnetvisserij op het IJsselmeer een groter aantal leeftijdsgroepen in de oogst de bestaande variatie veroorzaakt door variabele recrutering nauwelijks kan dempen. Op grond van de aantallen 0+ baars en snoekbaars in de aalkuil tijdens najaarsbemonsteringen kan de toekomstige oogst van een bepaalde jaarklasse worden voorspeld. Voor baars verschillen de boven- en ondergrens van het 95% betrouwbaarheidsinterval een factor 1.6 en voor snoekbaars een factor 2.7. Als gevolg van de grote variatie in jaarklassterkte en de onzekerheid in de oogstvoorspelling zal het praktisch onmogelijk zijn effecten van beheersmaatregelen aan te tonen, indien de toename in de oogst als gevolg van beheersmaatregelen zich alleen maar effectueert via een hogere gemiddelde opbrengst per recruit. De grootste oogstverbetering voor de kieuwnetvisserij wordt mogelijk verkregen door het vergroten van het paaiend bestand van met name snoekbaars. Een meer experimentele benadering van het beheer, zoals bijvoorbeeld het enige jaren sluiten van de visserij op het zuidelijk deel van IJsselmeer, zouden op dit punt meer inzichten kunnen verschaffen.

Chapter 1

INTRODUCTION TO THE THESIS

Eel (*Anguilla anguilla*), pikeperch (*Stizostedion lucioperca*) and perch (*Perca fluviatilis*) are the major fish species of commercial value for the Lake IJssel fishery. The stocks of pikeperch and perch are at present exploited by a commercial fishery which mainly uses 101 mm stretched mesh gill nets. According to Willemsen (1983), the pikeperch stock is growth-overfished. The present yield of pikeperch is very low and has always been highly variable (Buijse et al. 1991; Van Densen et al. 1990). Perch grows slower than pikeperch and recruits to the fishery at a higher age (Willemsen 1977), and appears to be more rationally exploited than pikeperch. A more rational, less intensive exploitation of pikeperch could at the same time result in a decline of the perch catches.

To exploit a fish stock, its dynamics should be quantified. The dynamics are a function of recruitment, growth, natural and fishing mortality and migration. Recruitment of pikeperch and perch in Lake IJssel is highly variable and the growth is rapid in comparison with other systems (Willemsen 1977). Natural mortality had yet not been quantified. Migration in and out of Lake IJssel was not taken into account in this study. The causes for variations in year-class strength and growth of pikeperch and perch in Lake IJssel and their implications for a rational exploitation of both species by the gill net fishery, aiming for yield maximisation and stabilisation, were subject of this study.

The methodology of this study consists of three parts: (1) analysis of long-term data sets, (2) collection and analysis of fishery-independent field data, and (3) model building. Data on the fish stocks in Lake IJssel have been collected mainly by means of experimental trawl surveys since 1966 by the Department of Coastal and Inland Fisheries and Cultures, Ministry of Agriculture, Nature Management and Fisheries (Steinmetz and Oudelaar 1971). Market sampling of the landings by the gill net fishery has been conducted since 1968 by the Netherlands Institute for Fishery Research in IJmuiden. Long-term data sets on water temperatures and weather conditions were used in the analysis. Field observations from 1987 to 1989 consisted of experimental trawl surveys to collect data on growth and abundance of the major fish species (except eel) and feeding habits of pikeperch, perch and smelt, and of water samples to collect data on abundance and size structure of the zooplankton. Model building comprised the development of a size- and age-structured model to evaluate management measures for enlargement and stabilisation of the yield of the gill net fishery.

This introduction starts with a description of the history of commercial fishery in Lake IJssel and continues with an outline of the various chapters of this thesis.

History of the Lake IJssel fishery with special attention to the exploitation of perch and pikeperch

Formerly Lake IJssel was an estuary named 'Zuiderzee'. The Zuiderzee was closed from the sea after being dammed in 1932. The rapid transition from brackish ($6 \text{ g Cl} \cdot \text{L}^{-1}$) in 1932 to fresh water ($0.2 \text{ g Cl} \cdot \text{L}^{-1}$) by 1937 (Havinga 1941) resulted in extreme changes in the fish stocks and in the fishery. The Zuiderzee fishery mainly exploited the stocks of anchovy (*Engraulis encrasicolus*), herring (*Clupea harengus*), eel, smelt (*Osmerus eperlanus*), flounder (*Platichthys flesus*) and shrimp (*Crangon crangon*) (Dorleijn 1987). Eel, smelt and flounder were the only species which were abundant before and after the lake became fresh. In the newly created Lake IJssel the fishery for eel was of main importance supplemented with those for pikeperch and perch. Land reclamation programmes reduced the area from its original 345,000 ha to its present 182,000 by the creation of three polders. This gradual reduction in surface area asked for an active policy to reduce the number of fishing companies to a level at which all of them were profitable (Anonymous 1956). In 1946 913 companies were involved in the fishery, while by 1981 there were only 119 companies left (Nagtegaal and Snel 1984).

After the damming of the inland sea the fishery was initially executed with both active fishing gear (bottom-trawls for eel, two-boat seines for pikeperch and perch) and passive fishing gear (fyke nets for eel and smelt, gill nets for pikeperch and perch, long lines for eel and beach seines for cyprinids) (Van Densen et al. 1990). Most active fishing gears have been banned through time; the two-boat seines in 1964 and the bottom-trawl in 1970. The bottom-trawl for eel was banned due to the large by-catch, which comprised, besides smelt and ruffe (*Gymnocephalus cernua*), large numbers of juvenile pikeperch and perch, but also because of requests by the sport fishery organisations, to whom the government attached an increasing importance (Bossaers 1987, p. 205). The ban on bottom-trawling is regarded the most drastic management measure in the history of the Lake IJssel fishery, because the landings of eel decreased sharply and to date never reached the level prior to 1970 (Van Densen et al. 1990). After the ban on trawling for eel fishermen switched towards eel-boxes and shoot-fyke nets, which are both placed in the open water area. At present trawling is allowed only for smelt provided it is used as bait for long lines and eel-boxes. Since the ban on two-boat seining the stocks of pikeperch and perch

in Lake IJssel are commercially exploited with gill nets mainly. Some perch are caught with fyke nets and long lines.

The fishery for eel has always been more important than that for other species, although the relative contribution of pikeperch, perch and smelt has increased since the ban on trawling in 1970 (Fig. 1). From 1947 to 1970 pikeperch and perch comprised together on average 11% (min.: 3% in 1967; max.: 19% in 1955) of the total outcome of the fishery, while from 1970 to 1990 the two species together comprised on average 32% (min.: 13% in 1970; max.: 47% in 1971). The increase in the contribution of percids is mainly a consequence of lower eel catches since 1970, and partly of the increased catches of perch (Table 1). The catches of pikeperch raised shortly after the ban on bottom-trawling, but the long-term average did not differ from the one prior to 1970. In the 1980s perch became more important than pikeperch for the fishery (Fig. 1).

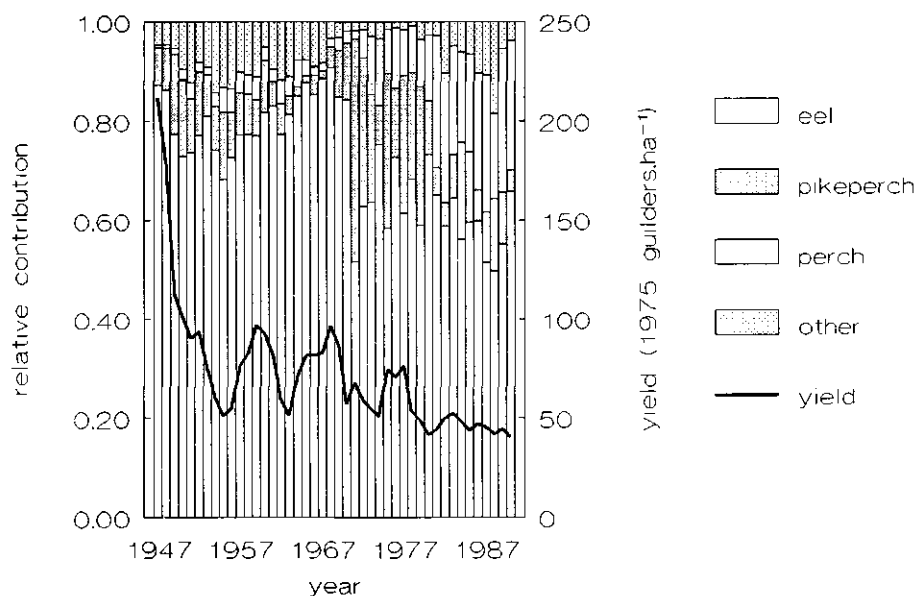


Fig. 1. Relative contribution by value of eel, pikeperch, perch and other fish to the yield of the commercial Lake IJssel fishery (left axis), and the outcome of this fishery in 1975-guilders.ha⁻¹ (right axis) over the period 1947-1990.

The catches of pikeperch and to a lesser extent those of perch have always been highly variable. After damming, the catches of pikeperch rose quickly from 1,5 tons in 1935 to 2,662 tons in 1939. The highest annual catch of pikeperch was 3,087 tons (10.4 kg.ha⁻¹) in 1949, while that of perch was 848 tons (4.2 kg.ha⁻¹) in 1981. The fishery for pikeperch has known three good

periods, which were always after events which had a large impact on the fishery: shortly after the damming, after World War II, and after the ban on bottom-trawling. In the early 1930s there was no specific fishery for pikeperch and perch. Only after the fish stocks had increased, more fishing companies started to exploit these species. Especially the high catches in 1939 resulted in a boom of the fishery (Havinga 1948a). Havinga estimated that in the season 1939-1940 80% of the legal-sized pikeperch were removed by the fishery. The fishery during World War II was hampered by a prohibition of bottom-trawling at night, a shortage of fishing materials, rations of oil, and claims of fishing boats for transport of military troops (Bossaers 1987 p. 183-187). Possibly, this has resulted in a recovery of the fish stocks and the fishery in the late 1940s.

Table 1. Mean long-term annual catches of eel, perch and pikeperch in kg.ha⁻¹ before and after the ban on bottom-trawling in 1970.

| | eel | pikeperch | perch |
|-----------|------|-----------|-------|
| 1947-1969 | 10.4 | 2.2 | 0.8 |
| 1970-1990 | 4.2 | 2.1 | 2.9 |

Compared with other systems the variation in yield is high for pikeperch and moderate for perch. The coefficient of variation in the annual yield over the period 1947-1987 was 95% and 76% and the year-to-year variation was 65% and 27% for pikeperch and perch respectively (Buijse et al. 1991). Already Havinga (1948a,b) argued that the high variation in the annual catches of pikeperch is due to variations in spawning success and to a high exploitation rate. The variation in year-class strength is larger for perch than for pikeperch (Chapter 3; Willemsen 1977). Nevertheless, the variation in yield is larger in pikeperch, because the catch consists of less age-groups due to the higher exploitation rate (Willemsen 1977).

Historically, the fishery for pikeperch and perch has only been regulated by means of mesh sizes and closed periods. An attempt was made to increase the mesh size to 100 mm in 1950. This measure has actually never been implemented due to protests by a cooperative association of Lake IJssel fishermen ('Coöperatieve Vereniging van IJsselmeervisschers'), who questioned the effectiveness of the measurement (Bossaers 1987 p. 191). Eventually the legal minimum mesh size was fixed at 92 mm stretched mesh by 1953 (Anonymous 1954, p. 35), and enlarged to 96 mm in 1967 (Van Densen et al. 1990). By 1972 the mesh size was enlarged to 104 mm, which after the introduction of a new measuring apparatus in 1974 was lowered to 101 mm

(Anonymous 1973, p. 237; Anonymous 1975, p. 255). Mesh size regulations for the gill net fishery have been based on length at maturity of female pikeperch and not on yield per recruit considerations. The gill net selection factor (total length of fish most effectively caught over the mesh size) for pikeperch is 0.48 (Van Densen 1987), which implies that 48 cm pikeperch are most efficiently caught in 101 mm gill nets, whereas 50% of the females are mature at 40 cm body length (Willemsen 1977). Until recently the effort was only limited by closed periods. The closed period for the gill net fishery was from 15 March to 1 July and since 1979 during weekends (Van Densen et al. 1990). By 1991 a gentleman's agreement among all fishing companies made it possible to standardise the effort per company to a maximum of 80 multifilament or 60 monofilament gill nets.

Standardisation of the recruitment indices

Recruitment of percids in Lake IJssel is indexed as the number of age 0 fish caught per standard trawl haul during autumn surveys. Age 0 fish have been sampled since 1966 by the Department of Coastal and Inland Fisheries and Cultures, Ministry of Agriculture, Nature Management and Fisheries. This survey is lake-wide covering multiple sites, and one haul is carried out at each site. Sampling has been standardised by gear type, towing speed and later also by haul duration. One characteristic of their survey was the large flexibility in when and where to sample. For instance, the survey was not carried out in a predefined week, but favourable sampling were awaited i.e. a period with high water turbidity due to wind action. It is common knowledge among fishermen that catches decrease with increasing water clarity. Decisions whether to sample or not were taken by the seat of one's pants, and sampling conditions during a trawl haul were recorded as good, moderate or bad (Steinmetz and Oudelaar 1971).

During the field observations from 1987 to 1989 the same sites were selected to be able to compare newly collected data with historical data sets collected from 1966 to 1986. The surveys during this period had to be planned one year in advance and thus sampling conditions had to be taken for granted. Consequently this sampling programme was never interrupted during periods of unfavourable sampling conditions. Therefore it was attempted to estimate the effect of water clarity on the catchability of fish in a bottom trawl.

Another routine trawl survey, conducted by the Netherlands Institute for Fisheries Research, offered the possibility to quantify the effect of variable water clarity on the catchability of six important freshwater fish species with a bottom trawl. This survey comprised multiple hauls in two selected areas. The results of this analysis are described in Chapter 2.

Causes for variations in growth and year-class strength

Fish populations vary because of density dependent and independent processes that determine recruitment, growth, and natural and fishing mortality (Sissenwine 1984). Koonce et al. (1977) give an overview of factors influencing year-class strength of percids. Explanatory factors given for the variation in year-class strength of pikeperch and walleye (*Stizostedion vitreum*) are rate of warming during springtime (Busch et al. 1975), lake level and temperature (Kallemeyn 1987), cannibalism and the absence of alternative prey (Forney 1976, 1980). Factors influencing year-class strength in perch or yellow perch (*Perca flavescens*) populations are temperature (Clady 1976; Henderson and Nepszy 1988; Kallemeyn 1987; Mills and Hurley 1990), wind damage to eggs (Clady 1976), lake level (Kallemeyn 1987), stock size (Henderson and Nepszy 1988, Mills and Hurley 1990), predation by pike (*Esox lucius*) in Windermere (Mills and Hurley 1990) and walleye in Oneida Lake (Nielsen 1980). Havinga (1948b) supposed that strong year-classes of pikeperch in Lake IJssel were produced in years when temperatures in May and June were above average. The variation in numbers of age 0 of pikeperch and perch during experimental fisheries in the 1940s illustrates the large variation in recruitment (Table 2). According to Willemsen (1977) recruitment and growth of pikeperch in Lake IJssel are positively influenced by high summer temperatures, whereas no clues were found for variations in recruitment of perch. For both species, a stock-recruitment relationship was not demonstrated by Willemsen (1977).

Long-term data sets exist on the fish stock in Lake IJssel, the water temperature and the wind velocity. To quantify the effect of water temperature, wind and stock biomass on the recruitment of pikeperch and perch a stepwise multiple regression analysis was carried out using these data sets (Chapter 3).

Causal mechanisms for the positive effect of high summer temperatures on recruitment of pikeperch have yet not been reported in the literature. The onset of piscivory as a year-class determining process has already been stressed for largemouth bass (Shelton et al. 1979; Timmons et al. 1980; Wicker and Johnson 1987) and pikeperch (Van Densen 1985). Wicker and Johnson (1987) related fat content and condition of largemouth bass to first-year survival. In Chapter 4 the condition of pikeperch is related to feeding, growth and survival of age 0 fish, and the effect of water temperature in relation to the onset of piscivory is discussed.

Chapter 5 gives a detailed description of the feeding habits of perch and the consequences for its growth. A generalised picture of the food and the growth has been given by Willemsen (1977). Up to 5 cm zooplankton is the most important food item, between 5 and 10 cm zooplankton and *Gammarus* spp., and over 10 cm smelt. Mean length at age in Lake IJssel was rapid compared

to other systems (Shafi and Maitland 1971; Thorpe 1977 p. 51). Deelder (1951) suggests that this rapid growth is due to the availability of smelt as a prey. In this chapter, the flexibility in the onset of piscivory is related to the availability of alternative prey. The relevance of this chapter for the management of the fishery is at present less than that of Chapters 3 and 4. However, studying the feeding habits of perch enlarged the insights in the dynamics of the ecosystem, especially the predator-prey relationship between perch and smelt. With this study it is possible to characterise the impact of the piscivorous perch on its own offspring and the buffering capacity of smelt as a fish prey, which information was used for the analysis of long-term data in Chapter 3. Such information is used for management decisions of the gill net fishery on perch in Lake Constance, where active adaptive management by means of flexible mesh size regulations is used to keep the stock of larger cannibalistic perch to a minimum to reduce its negative impact on recruitment (Staub and Krämer 1991).

Table 2. Mean number of age 0 pikeperch and perch per haul of 45 min during experimental fisheries with a fine-meshed beam-trawl in September 1938-1951. The figures for the years 1940-1943 are less reliable, because in these years the number of hauls was low (Havinga 1954).

| year | pikeperch | perch |
|------|-----------|-------|
| 1938 | 5 | |
| 1939 | 53 | |
| 1940 | 25 | 102 |
| 1941 | 171 | 334 |
| 1942 | 3 | 2 |
| 1943 | 39 | 48 |
| 1946 | 9 | 0 |
| 1947 | 277 | 191 |
| 1948 | 134 | 6 |
| 1949 | 40 | 2 |
| 1950 | 188 | 11 |
| 1951 | 26 | 192 |

Coping with uncertainty

Uncertainty in the nature of the processes, which underlie recruitment variability and in the expected levels of recruitment has important implications for fisheries management (Sissenwine et al. 1988). The increased knowledge on the processes governing the formation of year-class strength of pikeperch and perch, described in Chapters 3 to 5, is a basis for the evaluation whether the year-class strength of percids can be managed. From a manager's point of view the processes that can be influenced by proper management are of particular interest.

To evaluate the consequences of growth, mortality and recruitment on the rational exploitation of pikeperch and perch in Lake IJssel, a size- and age-structured simulation model has been developed using parameters on the population dynamics of these species. In Chapter 6 a description of the model is given. At present all processes in the model are density-independent. Growth is described as a function of size and temperature and mortality as a function of size. The consequences of management measures for the decline during the transitional period after implementation of a measure and the eventual gain in a higher yield per recruit are discussed. Chapter 7 finally integrates the information collected on recruitment variability, and discusses the feasibility to stabilise the yield to a certain desired level in the light of constant effort policy and uncertainties in yield predictions.

REFERENCES

- Anonymous 1954. Jaarcijfers over de visserij gedurende het jaar 1953. Verslagen en Mededelingen van de Directie van de Visserijen 45. Ministerie van Landbouw, Visserij en Voedselvoorziening. 126 p.
- Anonymous 1956. De versnelde beperking van het aantal houders van vergunningen voor de visserij op het IJsselmeer. Visserijnieuws 8: 193-195.
- Anonymous 1973. Jaarverslag 1972 (Annual report 1972). Visserij; voorlichtingsblad voor de Nederlandse visserij 26: 211-322 + tables. Ministerie van Landbouw en Visserij. Directie van de Visserijen.
- Anonymous 1975. Jaarverslag 1974 (Annual report 1974). Visserij; voorlichtingsblad voor de Nederlandse visserij 28: 223-364 + tables. Ministerie van Landbouw en Visserij. Directie van de Visserijen.
- Bossaers, K.W.J.M. 1987. Zuiderzeevissers: geschiedenis van de belangenorganisaties van de vissers op Zuiderzee en IJsselmeer. Publicatie van de Stichting voor het Bevolkingsonderzoek in de drooggelegde Zuiderzeepolders dl. 52. De Walburg Pers, Zutphen. 272 p.
- Buijse, A.D., W.L.T. van Densen, and M.A.M. Machiels. 1991. Characteristics in the inter-annual variation of the yield from the professional fishery in freshwater bodies of the temperate and the tropical zone. p. 305-322. In I.G. Cowx [ed.] Catch effort sampling strategies and their application in freshwater fisheries management. Fishing News Books, Blackwell Scientific Publications. Oxford.

- Busch, W.-D. N., R.L. Scholl, and W.L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in Western Lake Erie, 1960-70. *J. Fish. Res. Board Can.* 32: 1733-1743.
- Clady, M.D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. *J. Fish. Res. Board Can.* 33: 1887-1893.
- Deelder, C.L. 1951. A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. *Hydrobiologia* 3: 357-378.
- Densen, W.L.T. van. 1985. Piscivory and the development of bimodality in the size distribution of 0+ pikeperch (*Stizostedion lucioperca* L.). *J. Appl. Ichthyol.* 1: 119-131.
- Densen, W.L.T. van. 1987. Gillnet selectivity to pikeperch, *Stizostedion lucioperca* (L.), and perch, *Perca fluviatilis* L., caught mainly wedged. *Aquacult. and Fish. Manage.* 18: 95-106.
- Densen, W.L.T. van, W.G. Cazemier, W. Dekker, and H.G.J. Oudelaar. 1990. Management of the fish stocks in Lake IJssel, the Netherlands. p. 313-327. *In* W.L.T. van Densen, B. Steinmetz, and R.H. Hughes [eds.] Proceedings of a symposium organized by the European Inland Fisheries Advisory Commission, Göteborg, Sweden 31 May - 3 June 1988. PUDOC, Wageningen.
- Dorleijn, P. 1987. Zuiderzeevervisserij in beeld. Publicatie van de Stichting voor het Bevolkingsonderzoek in de drooggelegde Zuiderzeepolders nr. 51. Amsterdam. De Walburg Pers. 143 p.
- Forney, J.L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966-73. *J. Fish. Res. Board Can.* 33: 783-792.
- Forney, J.L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. *NY. Fish Game J.* 27: 105-141.
- Havinga, B. 1941. De veranderingen in den hydrographischen toestand en in de macrofauna van het IJsselmeer gedurende de jaren 1936-1940. *Meded. Zuiderzee Commissie* 5: 5-26.
- Havinga, B. 1948a. De ontwikkeling van de visstand in het IJsselmeer. *Visserijnieuws* 1: 30-32.
- Havinga, B. 1948b. De ontwikkeling van de visstand in het IJsselmeer. *Visserijnieuws* 1: 45-47.
- Havinga, B. 1954. Vissen. p. 253-267. *In* L.F. De Beaufort [ed.] Veranderingen in de flora en fauna van de Zuiderzee (thans IJsselmeer) na de afsluiting in 1932. Nederlandse Dierkundige Vereniging.
- Henderson, B.A., and S.J. Nepszy. 1988. Recruitment of yellow perch (*Perca flavescens*) affected by stock size and water temperature in Lakes Erie and St. Clair, 1965-85. *J. Great Lakes Res.* 14: 205-215.
- Kallemeyn, L.W. 1987. Correlations of regulated lake levels and climatic factors with abundance of young-of-the-year walleye and yellow perch in four lakes in Voyageurs National park. *N. Am. J. Fish. Manage.* 7: 513-521.
- Koonce, J.F., T.B. Bagenal, R.F. Carline, K.E.F. Hokanson, and M. Nagiec. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. *J. Fish. Res. Board Can.* 34: 1900-1909.
- Mills, C.A., and M.A. Hurley. 1990. Long-term studies on the Windermere populations of perch (*Perca fluviatilis*), pike (*Esox lucius*) and Arctic charr (*Salvelinus alpinus*). *Freshw. Biol.* 23: 119-136.

- Nagtegaal, P., and H.J. Snel. 1984. De beroepsvisserij in het IJsselmeergebied. Rijksdienst voor de IJsselmeerpolders. Ministerie van Verkeer en Waterstaat. Rapport 1984 - 14 abw. 76 p.
- Nielsen, L.A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. J. Fish. Res. Board Can. 37: 11-19.
- Shafi, M., and P.S. Maitland. 1971. The age and growth of perch (*Perca fluviatilis* L.) in two Scottish lochs. J. Fish Biol. 3: 39-57.
- Shelton, W.L., W.D. Davies, T.A. King, and T.J. Timmons. 1979. Variation in growth of the initial year class of largemouth bass in West Point Reservoir, Alabama and Georgia. Trans. Am. Fis. Soc. 108: 142-149.
- Sissenwine, M.P. 1984. Why do fish populations vary? In: R.M. May [ed.] Exploitation of marine communities. Dahlem Konferenzen. Life Sciences Res. Rep. 32. Springer-Verlag. Berlin. p. 59-94.
- Sissenwine, M.P., M.J. Fogarty, and W.J. Overholtz. 1988. Some fisheries management implications of recruitment variability. p. 129-152. In J.A. Gulland [ed.] Fish population dynamics: the implications for management. second edition. John Wiley & Sons. Chichester.
- Staub, E., and A. Krämer. 1991. Grossversuch mit 28mm-Netzen zur Befischung der Wachstumverzögerten Barschkohorte 1988. SVA/IBK 27 p. + appendices.
- Steinmetz, B., and H.G.J. Oudelaar. 1971. IJsselmeer proefvisserijen met de grote kuil. Jaren 1966 t/m 1969. Hoofdafdeling Sportvisserij en Beroepsbinnenvisserij. Utrecht. Documentatie-rapporten no. 13. 11 p.
- Thorpe, J. 1977. Synopsis of biological data on the perch, *Perca fluviatilis* Linnaeus, 1758 and *Perca flavescens* (Mitchill, 1814). FAO Fish. Synop. no. 113. vii + 138 p.
- Timmons, T.J., W.L. Shelton, and W.D. Davies. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama and Georgia. Trans. Am. Fish. Soc. 109: 176-186.
- Wicker, A.M., and W.E. Johnson. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. Trans. Am. Fish. Soc. 116: 264-271.
- Willemsen, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34: 1710-1719.
- Willemsen, J. 1983. Biology and management of pikeperch. Proc. 3rd. Brit. Fresw. Fish. Conf., Univ. of Liverpool. p. 115-125.

Chapter 2

THE INFLUENCE OF WATER CLARITY ON THE CATCHABILITY OF SIX FRESHWATER FISH SPECIES IN BOTTOM TRAWLS.

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ABSTRACT

Bottom trawl surveys are carried out every autumn to estimate the relative abundance of six major fish species, especially that of pikeperch (*Stizostedion lucioperca*) and Eurasian perch (*Perca fluviatilis*), in the 182,000-ha Lake IJssel. The catchability of these species is influenced by light intensity at the bottom and therefore by water clarity and water depth. In autumn, water clarity can differ greatly from day to day because of wind-mediated re-suspension of sediments. Catchability of ruffe (*Gymnocephalus cernua*) and age 0 pikeperch showed a significant inverse relationship with light intensity at the bottom and, therefore, a correction should be made when catch data for these species are used to estimate population size or year-class strength. Results were not consistent for perch, while for smelt (*Osmerus eperlanus*), roach (*Rutilus rutilus*) and bream (*Abramis brama*) the influence of light intensity upon catchability was not significant. Corrected and uncorrected estimates of the abundance of age 0 pikeperch, based on trawl samples, were compared to demonstrate the effect of water clarity on the estimation of year-class strength. Increased water clarity can lead to zero catches and consequently diminish the effectiveness of sampling programmes.

INTRODUCTION

Bottom trawling is a well known technique for sampling fish stocks (e.g. Sissenwine et al. 1983). Catches are usually standardised as catch per unit effort (CPUE). Catchability or gear efficiency, however, can vary with environmental conditions; thus temperature influences swimming performance (Wardle 1983), and water clarity can influence the vertical distribution of fish (Bohl 1980) or trawl visibility (Glass and Wardle 1989). Much attention is given to fish behaviour in relation to towed fishing gear (Wardle 1983) and marine cinematographic studies have revealed that sight is the most important factor in gear detection by fish (Glass and Wardle 1989).

The effects of varying light conditions on the catchability of fish species have seldom been quantified and experiments are mostly limited to the comparison of day and night hauls (Butterworth and Coles 1977; Quinn and Kojis 1987). Differences in catch rates are often due to changes in the vertical distribution of fish (e.g. Atkinson 1989; Bohl 1980). Catchability can decrease at night ($<10^{-6}$ lx) because the herding effect of the sweeps of the trawl disappears and during daytime because of early detection of the gear at high light levels (>1 lx) (Glass and Wardle 1989). Thus, mid-water trawl efficiency for sockeye salmon (*Oncorhynchus nerka*) during night hauls was inversely related to ambient light, varying with lunar phase and cloudiness (Robinson and Barraclough 1978). Lower water clarity, during day hauls, is thought to have increased CPUE threefold in trawls of yellow perch (*Perca flavescens*) in Oneida Lake (Nielsen 1983). Light conditions during the day can vary considerably over short periods due to re-suspension of sediments by wind (Carper and Bachmann 1984).

Bottom trawl surveys are carried out in Lake IJssel every autumn to estimate the relative abundance of six major fish species. Our objective was to study the effects of variations in light conditions near the bottom on catchability of the six major freshwater fish species caught during the day with a bottom trawl. The species concerned were European smelt (*Osmerus eperlanus*), bream (*Abramis brama*), roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernua*), and especially Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*).

MATERIALS AND METHODS

Description of the area

Lake IJssel is a large and shallow eutrophic lake, formerly an inland sea, divided into a northern (112,000 ha) and southern basin (70,000 ha) by the construction of a dyke in 1975 (Fig. 1). The northern basin has an average

depth of 4.5 m, with depressions up to 10 m deep caused by former tidal movements. The southern basin has an average depth of 3.6 m. Water clarity in both parts varies between 0.1 and 2 m Secchi disk depth, averaging 0.65 m. In both basins, the average water temperature is 10.4°C and varies annually from 0 to 25°C. Total-P is 0.22 mg.L⁻¹. These and other physicochemical parameters are described by Willemsen (1977).

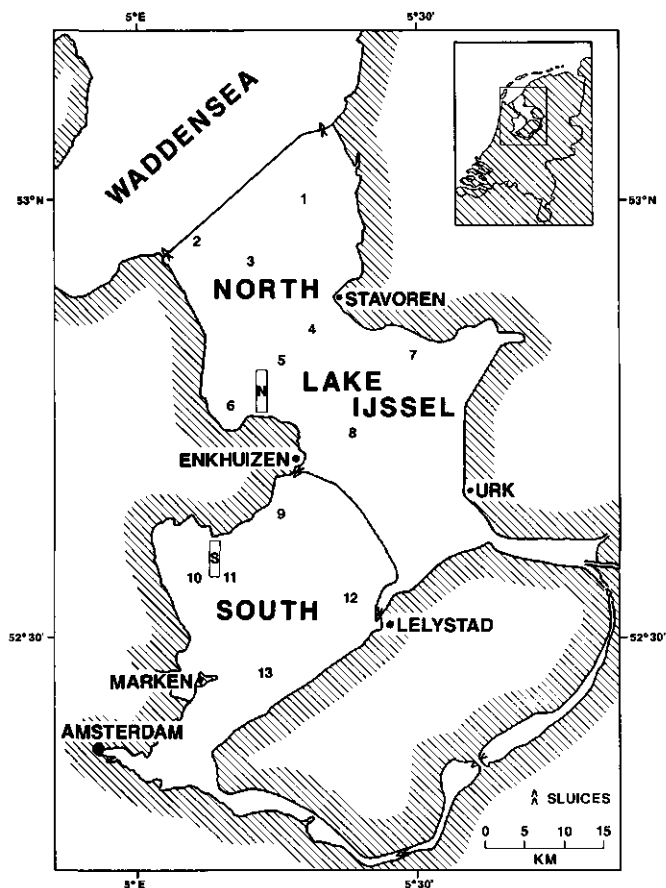


Fig. 1 Netherlands Institute for Fisheries Research bottom trawl sampling areas Wagenpad (N) and Hoornse Hop (S) at Lake IJssel. Regular stations of the lake-wide survey (1-13), which was carried out by the Department of Coast-, Inland Fisheries and Cultures, Ministry of Agriculture and Fisheries.

In Lake IJssel, the influence of wind on water clarity is most pronounced in autumn and winter when algal densities are low. During lake-wide survey trawling in the period 1966-1987 sampling was started when Secchi disk

readings were about 0.8 m or less assuming constant catchability. In years when water stayed clear (over 0.8 m Secchi disk depth) sampling was ultimately carried out irrespective of water clarity, but corrections for the assumed lower catchability could not be made.

Surveys

Two types of bottom trawl surveys are carried out in Lake IJssel in the autumn of every year to estimate the abundance of the major fish species:

Survey I - two-areas survey

A trawl survey was made in two selected areas that were homogeneous in depth and bottom type: "Wagenpad" (N), in the northern part, and "Hoornse Hop" (S), in the south (Fig. 1). Within each area multiple hauls were made at varying distances parallel to the shore. Data were analysed for 1981-1988. Area N was sampled every year, while area S was not sampled in 1984 and 1987.

Under the assumption that within these areas fishes were homogeneously distributed, quantitative effects of water clarity on the catchability of fish species were estimated using data from this survey.

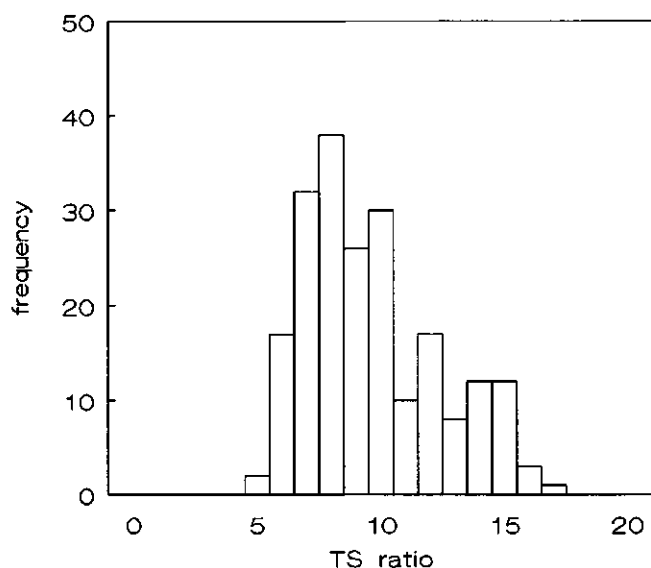


Fig. 2 Frequency distribution of total water depth: Secchi depth ratios (TS) in survey I. N = 208.

Area N was sampled within 12 days every year in which 13 to 27 hauls were made and at distances from the shore varying from 200 to 5400 m. Total depths at the sampling sites ranged from 4.5 to 6.5 m and Secchi disk readings from 0.4 to 1.1 m (Table 1). In area S similar data were collected in a 2-day period using eight to 13 hauls. Distance from shore varied between 500 and 5000 m; total depth ranged between 3.4 and 4.0 m and Secchi depth between 0.25 and 0.70 m (Table 2). In area S Secchi depth readings did not vary in 1981 and in 1982; therefore, these years were omitted from the analyses. The start of the first and last trawl haul were at 8:35 h and at 15:45 h respectively. The ratio between total water depth and Secchi disk readings varied between 5 and 17 (Fig. 2).

Survey II - lake-wide survey

From 1966 until 1989 a lake-wide trawl survey covering eight stations in the northern part and five stations in the southern part of Lake IJssel was made (Fig. 1). At each station a single haul was taken. Data from this survey are used here to demonstrate the problem of varying catchability as a consequence of variations in water clarity in general and to show the effect of correcting catches for variations in catchability on the estimation of the year-class strength (YCS) of pikeperch.

During both surveys the abundance of the commercially important perch and pikeperch was indexed by the mean number of age 0 fish caught per standard haul, but the weights of the catches of other species were also recorded. Trawling was carried out with a bottom trawl (cod-end 20-mm stretched mesh, upper-rope 13 m; bottom rope 14.75 m). The trawl was kept open with an 8-m broad beam and two 1-m high danlenos, and pulled at an average speed of $1.6 \pm 0.1 \text{ m.s}^{-1}$. Haul duration was 10 min. For the lake-wide survey haul duration varied in the early years between 15 and 45 minutes, but was standardised at 10 min from 1982 onwards. Only day hauls were made. Night hauls were impossible because commercial gill nets and fyke nets could not be avoided.

The fish were sorted by species on deck and weighed to the nearest 0.1 kg. To distinguish age 0 pikeperch and age 0 and age 1 perch from their length-frequency distribution, individual perch and pikeperch were measured to the nearest cm total length.

Table 1.

Station location and catch characteristics of bottom trawls at area N in the period 1981-1988. N = number of hauls; gr = age-group; min. = minimum and max. = maximum (date = first and last day of sampling; time = earliest and latest hour of sampling); blanks = no data.

| year | n | date | time | distance from shore (m) | water depth (m) | Secchi depth (m) | perch gr 0 (n) | perch gr 1 (n) | perch gr ≥ 2 (n) | pikeperch gr 0 (n) | ruffe (kg) | smelt (kg) | roach (kg) | bream (kg) |
|------|----|----------------|-------|-------------------------------|-----------------------|------------------------|----------------------|----------------------|------------------------|--------------------------|--------------------|--------------------|---------------|---------------|
| 81 | 13 | min. 12-Oct | 08:34 | | 5.5 | 0.40 | 5 | 56 | 18 | 1 | 1.0 | 5.5 | 7.7 | 1.3 |
| | | mean 11:47 | | 5.8 | 0.58 | | 21 | 208 | 49 | 19 | 7.4 | 27.8 | 26.0 | 54.7 |
| | | max. 22-Oct | 15:15 | | 6.0 | 0.85 | 43 | 681 | 120 | 49 | 23.1 | 66.5 | 56.1 | 192.0 |
| 82 | 20 | min. 11-Oct | 09:00 | | 5.5 | 0.40 | 13 | 0 | 6 | 4 | 0.1 | 8.6 | 0.6 | 0.1 |
| | | mean 12:22 | | 5.7 | 0.66 | | 38 | 5 | 77 | 25 | 2.0 | 20.8 | 37.7 | 21.1 |
| | | max. 14-Oct | 15:45 | | 6.0 | 0.80 | 97 | 18 | 197 | 104 | 8.6 | 33.0 | 73.2 | 59.5 |
| 83 | 17 | min. 18-Oct | 09:04 | | 4.5 | 0.40 | 178 | | | 2 | 0.6 | 4.8 | 6.9 | 1.8 |
| | | mean 12:42 | | 5.8 | 0.70 | | 505 | | | 116 | 7.0 | 12.8 | 38.2 | 31.9 |
| | | max. 27-Oct | 14:39 | | 6.3 | 0.90 | 2412 | | | 497 | 59.1 | 23.8 | 81.3 | 66.6 |
| 84 | 25 | min. 22-Oct | 08:45 | 200 | 4.5 | 0.60 | 1 | 4 | 0 | 2 | 0.1 | 0.3 | 2.3 | 0.0 |
| | | mean 12:03 | | 2090 | 5.9 | 0.84 | 58 | 71 | 60 | 21 | 1.0 | 10.4 | 37.2 | 63.0 |
| | | max. 01-Nov | 15:19 | 5400 | 6.5 | 1.00 | 134 | 185 | 183 | 64 | 4.2 | 40.1 | 81.0 | 172.0 |
| 85 | 20 | min. 28-Oct | 08:40 | 350 | 5.3 | 0.60 | 152 | | | 1 | 0.2 | 2.1 | 3.2 | 0.9 |
| | | mean 11:45 | | 1999 | 5.8 | 0.83 | 1742 | | | 5 | 6.2 | 7.4 | 32.5 | 68.8 |
| | | max. 08-Nov | 14:55 | 4000 | 6.5 | 1.10 | 5072 | | | 12 | 29.8 | 17.7 | 110.0 | 225.0 |
| 86 | 27 | min. 27-Oct | 08:49 | 250 | 5.2 | 0.40 | 402 | 213 | 5 | 3 | 4.9 ^{a)} | 5.1 ^{a)} | 2.0 | 6.9 |
| | | mean 11:31 | | 1957 | 6.0 | 0.49 | 900 | 924 | 37 | 16 | 13.5 ^{a)} | 14.1 ^{a)} | 29.2 | 91.1 |
| | | max. 06-Nov | 15:19 | 4000 | 6.5 | 0.70 | 1564 | 1493 | 71 | 49 | 22.0 ^{a)} | 29.8 ^{a)} | 100.0 | 405.0 |
| 87 | 19 | min. 26-Oct | 08:55 | 250 | 5.5 | 0.50 | 51 | 251 | 37 | 0 | 0.5 | 3.5 | 0.7 | 1.5 |
| | | mean 12:00 | | 1684 | 5.9 | 0.72 | 140 | 881 | 386 | 5 | 13.9 | 18.0 | 19.7 | 59.9 |
| | | max. 29-Oct | 14:34 | 3500 | 6.2 | 0.95 | 310 | 2072 | 533 | 13 | 24.9 | 39.9 | 46.3 | 485.0 |
| 88 | 26 | min. 31-Oct | 09:10 | 250 | 5.0 | 0.60 | 13 | 1 | 43 | 1 | 1.0 | 1.9 | 0.8 | 0.0 |
| | | mean 12:10 | | 1837 | 5.8 | 0.79 | 68 | 9 | 228 | 11 | 11.9 | 8.6 | 7.6 | 19.9 |
| | | max. 03-Nov | 14:55 | 4000 | 6.2 | 1.00 | 145 | 24 | 439 | 30 | 35.0 | 17.0 | 26.0 | 163.4 |

a) Ruffe and smelt catches in area N in 1986 were separated only for 11 out of the 27 hauls. A subset of these 11 hauls was used to standardise the independent variables for use in the multiple regression analysis of the effects of the independent variables on the catches of those two species.

Table 2. Station location and catch characteristics of bottom trawls at area S in 1983, 1985, 1986 and 1988. N = number of hauls; gr = age-group; min. = minimum and max. = maximum (date = first and last day of sampling; time = earliest and latest hour of sampling); blanks = no data.

| year | n | date | time | distance from shore (m) | water depth (m) | Secchi depth (m) | perch gr 0 (n) | perch gr 1 (n) | perch gr ≥2 (n) | ruffe (kg) | smelt (kg) | roach (kg) |
|------|----|--------|-------|-------------------------------|--------------------|------------------------|----------------------|----------------------|-----------------------|---------------|---------------|---------------|
| 83 | 8 | 20-Oct | 09:40 | | 3.8 | 0.40 | 23 | 150 | 5 | 3.4 | 1.1 | 1.4 |
| | | | 12:30 | | 3.9 | 0.44 | 79 | 356 | 18 | 9.0 | 2.4 | 8.5 |
| | | 21-Oct | 15:04 | | 4.0 | 0.50 | 145 | 519 | 36 | 15.9 | 3.3 | 25.1 |
| 85 | 10 | 06-Nov | 09:04 | 500 | 3.4 | 0.30 | 155 | 23 | 22 | 7.0 | 5.3 | 1.6 |
| | | | 10:59 | 2750 | 3.8 | 0.34 | 279 | 75 | 63 | 10.8 | 9.7 | 7.0 |
| | | 07-Nov | 13:55 | 5000 | 4.0 | 0.35 | 408 | 159 | 97 | 18.3 | 18.1 | 13.2 |
| 86 | 10 | 28-Oct | 09:19 | 500 | 3.7 | 0.25 | 47 | 156 | 35 | 11 | 2.1 | 2.1 |
| | | | 11:55 | 2750 | 3.9 | 0.30 | 426 | 195 | 59 | | | 5.5 |
| | | 29-Oct | 14:30 | 5000 | 4.0 | 0.35 | 967 | 292 | 103 | | | 8.5 |
| 88 | 13 | 09-Nov | 09:45 | 500 | 3.6 | 0.40 | 4 | 1 | 19 | 4.4 | 1.6 | 0.8 |
| | | | 12:30 | 2385 | 3.8 | 0.48 | 47 | 5 | 49 | 17.7 | 3.9 | 2.6 |
| | | 10-Nov | 15:10 | 4000 | 3.9 | 0.70 | 134 | 12 | 74 | 36.2 | 7.3 | 6.5 |

Data treatment and analysis

The analysis of data collected with survey I comprised three procedures: 1. transformation of data, 2. multiple regression analysis to determine which indicator variables contributed significantly to catch variation and 3. construction of a model for correcting catches for the effects of water clarity on catchability, which had lake-wide applicability.

Although the sampling areas N and S were regarded as homogeneous with respect to the fish distribution during the survey, and mortality during the survey was assumed to be negligible, distance from shore and chronological haul number (during one survey within one area) were also included in the analyses. Time of day was included to investigate the influence of incoming light and is expressed as the sine of the angle of the sun altitude. Data are lacking on distance to the shore for area N in 1981-83 and for area S in 1983. These years were therefore not included in the multiple regression analysis. They were included for the construction of a model, which corrects catches for effects of water clarity.

In this study the effect of within-year variations in water clarity and other independent variables on the bottom trawl catches is analysed. To generate a model which uses data from various years, both the dependent and the independent variables were standardised for their 'within-year mean', because year-to-year variations in fish abundance caused by e.g. year-class strength variations would otherwise obscure the effect of the variables on the catches. Results will thus express the relative effect of water clarity on the catchability, and can be used to calculate indices of fish abundance at a reference water clarity.

Catches from areas N and S were transformed to the natural log of the ratio of the catch from one haul to the geometric mean catch of all hauls within the area in the same year.

$$Cs_{ij} = \log_e(C_{ij}/C_j) \quad (1)$$

where:

- Cs = standardised catch, for mean abundance per year, which is log-transformed;
- C = catch in number (perch and pikeperch) or kg (other species) per 10-min trawl haul;
- i = haul number in year j .

Following Pennington (1983) data were first divided into zero and non-zero catches. Only non-zero values (1066 of 1075 sets for all species) were used for

parameter estimation. Bream catch data for area S were not analysed, since they comprised 25% zero catches.

Light intensity at the bottom, where the trawl sampled, was not measured directly and is expressed relative to the incident daylight intensity at the water surface with the ratio between total water depth and Secchi depth, which ratio is further referred to as light intensity. Variations in surface light due to cloudiness at the time of sampling are unknown but assumed to be negligible compared to the effect of varying water clarity. Secchi disk depth can be approximated by the depth of 20% surface light (Lorenzen 1980). So the ratio between the depth of a water and Secchi disk depth is the n^{th} power of 0.2ⁿ and indicates the fraction of surface light, which reaches the bottom. The total water depth: Secchi depth (TS) ratios were standardised by subtracting the 'within-year mean ratio':

$$TSs_{ij} = (T/S)_{ij} - (T/S)_j \quad (2)$$

where:

TSs = standardised total water depth: Secchi depth ratio
T = total water depth (m)
S = Secchi depth (m)

The independent variables 'distance to the shore' and 'time of day' were similarly standardised by subtracting the 'within-year mean'. With this standardisation of the variables, data from various years are brought to the same scale (mean = 0) and can consequently be pooled for regression analysis.

To generate a model, which corrects catches for varying catchability and which is applicable lake-wide, water clarity was the only useful parameter of this study which could be included. Therefore the following model (intercepts were never significant) was calculated:

$$Cs = a * TSs \quad (3)$$

where:

a = constant

The estimated parameter 'a' can be used to standardise all data from every year and sampling site, to one TS ratio, through which a better comparison can be made of variations of catch over time and distribution:

$$Cr_{ij} = C_{ij} * e^{a * (TSr - (T/S)_{ij})} \quad (4)$$

where:

Cr = catch standardised to a reference total water depth: Secchi depth ratio

TSr = reference total water depth: Secchi depth ratio

The reference total water depth: Secchi depth ratio was calculated as the overall-mean of this ratio measured during the lake-wide survey.

RESULTS

Catches tend to decline with increasing light intensity at the bottom as exemplified for catches of ruffe during the lake-wide survey (Fig. 3). It is not possible to quantify the effect of light intensity on the catchability of ruffe from these data, because catches are a function of local abundance at the sampling sites as well as catchability.

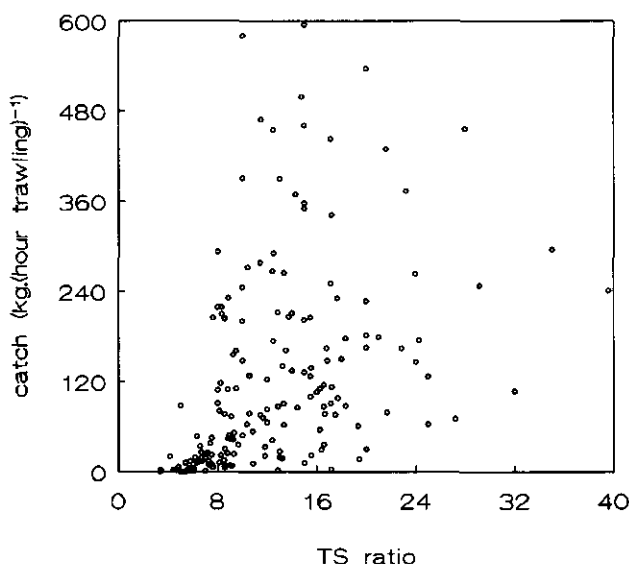


Fig. 3 Trawl catches of ruffe vs the total water depth: Secchi depth ratio (TS) during survey II at the northern part of Lake IJssel, 1966-1989. N = 170.

Catches of six species varied largely within the selected areas N and S (Tables 1 and 2). Within year, the minimum variation was less than fivefold for all species except bream and the maximum variation was more than hundredfold for all species except for age 1 perch. Among years catches varied more than

hundredfold for age 2 and older perch, age 0 pikeperch, ruffe, smelt and roach and more than thousandfold for age 0 and 1 perch and bream.

Table 3. Correlation matrix of the standardised catches of six fish species with total water depth: Secchi depth ratio (TS), distance from shore (DI), chronological haul number (HANO) and time of day (TI) at area N. N = number of hauls; * $p < 0.05$; ** $p < 0.01$.

| SPECIES | AGE-GROUP | N | TS | DI | HANO | TI |
|-----------|-----------|-----|----------|----------|--------|--------|
| PERCH | 0 | 117 | 0.287** | -0.027 | 0.035 | -0.090 |
| PERCH | 1 | 97 | 0.220** | 0.215* | -0.102 | -0.022 |
| PERCH | ≥2 | 96 | -0.058 | 0.474** | -0.032 | -0.120 |
| PIKEPERCH | 0 | 115 | 0.522** | -0.221* | -0.157 | 0.155 |
| RUFFE | ALL | 100 | 0.399** | 0.213* | 0.017 | -0.163 |
| SMELT | ALL | 101 | 0.281** | -0.257** | -0.084 | 0.173 |
| ROACH | ALL | 117 | 0.146 | 0.247* | -0.023 | -0.157 |
| BREAM | ALL | 115 | 0.179 | -0.323** | -0.051 | -0.013 |
| DI | | 117 | -0.099 | | | |
| HANO | | 117 | -0.400** | 0.043 | | |
| TI | | 117 | -0.013 | -0.424** | 0.110 | |

Table 4. Correlation matrix of the standardised catches of five fish species with total water depth: Secchi depth ratio (TS), distance from shore (DI), chronological haul number (HANO) and time of day (TI) at area S. N = number of hauls; * $p < 0.05$; ** $p < 0.01$.

| SPECIES | AGE-GROUP | N | TS | DI | HANO | TI |
|-----------|-----------|----|---------|---------|----------|--------|
| PERCH | 0 | 33 | 0.707** | 0.220 | -0.186 | 0.297 |
| PERCH | 1 | 33 | 0.642** | 0.316 | -0.456** | 0.080 |
| PERCH | ≥2 | 33 | 0.421** | 0.264 | -0.280 | -0.025 |
| PIKEPERCH | 0 | 30 | 0.524** | 0.180 | -0.251 | -0.186 |
| RUFFE | ALL | 23 | 0.577** | 0.066 | -0.272 | 0.295 |
| SMELT | ALL | 23 | 0.479* | -0.423* | -0.439* | -0.088 |
| ROACH | ALL | 33 | 0.120 | 0.178 | -0.270 | -0.295 |
| DI | | 33 | 0.322 | | | |
| HANO | | 33 | -0.179 | 0.075 | | |
| TI | | 33 | 0.264 | 0.231 | 0.059 | |

To compare the significance of the independent variables on standardised catches one correlation matrix was calculated for each fish category. Catches increased with decreasing light intensity at the bottom, as shown by the significant positive correlation between catches and TS ratio, for all fish categories except for roach, bream and age 2 and older perch in area N (Table 3) and for roach in area S (Table 4). The significant correlation between catches per fish category and distance to shore showed that in area N age 1 and older perch, and ruffe and roach were common more off-shore, while age 0 pikeperch, smelt and bream were common more inshore. Also in area S smelt

catches were highest inshore. No negative trend was found in the catches during the sampling period, except for smelt and age 2 and older perch, so mortality during the survey periods was not manifest. Catches did not correlate with time of day. So within the period of a day that trawls were made, effects of varying light conditions due to the changing altitude of the sun on the catchability were negligible.

Correlations among the independent variables showed a significant negative correlation between TS ratio and haul number in area N, which is due to the sampling strategy of starting when circumstances were favourable. A spurious correlation was found between time of day and distance from shore in area N.

Using only those independent variables which were significant ($p < 0.05$) in a multiple regression, 6% (roach) to 31% (age 0 pikeperch) of the variance in catch data could be explained for area N, and 18% (age 2 and older perch) to 53% (age 1 perch) for area S (Table 5). Only light intensity and distance from shore contributed considerably to the explanation of the variation in the catches in the areas N and S.

Table 5. Significant ($p < 0.05$) variables explaining variance in catch data of six fish species and fraction of variance explained within two areas N and S of Lake IJssel. R^2 = fraction variance explained; DI = distance from shore; HANO = chronological haul number; TS = total water depth: Secchi depth ratio.

| SPECIES | AGE-GROUP | Area N VARIABLES | R^2 | Area S VARIABLES | R^2 |
|-----------|-----------|---------------------|-------|---------------------|-------|
| PERCH | 0 | TS | 0.08 | TS | 0.50 |
| PERCH | 1 | TS, DI | 0.11 | TS, HANO | 0.53 |
| PERCH | ≥ 2 | DI | 0.22 | TS | 0.18 |
| PIKEPERCH | 0 | TS, DI | 0.31 | TS | 0.27 |
| RUFFE | ALL | TS, DI | 0.23 | TS | 0.33 |
| SMELT | ALL | TS, DI | 0.13 | TS, DI | 0.50 |
| ROACH | ALL | DI | 0.06 | | |
| BREAM | ALL | DI | 0.10 | | |

Correction factors for catches made during the lake-wide survey could only be calculated using the TS ratio, which varied between similar ranges both inshore and offshore. The effect of distance from shore on the catches cannot be extrapolated lake-wide (Fig. 1). It is realised that by keeping light intensity as the only explanatory variable, its effect can be overestimated, if the explanatory capability is incorrectly taken over from the excluded variables.

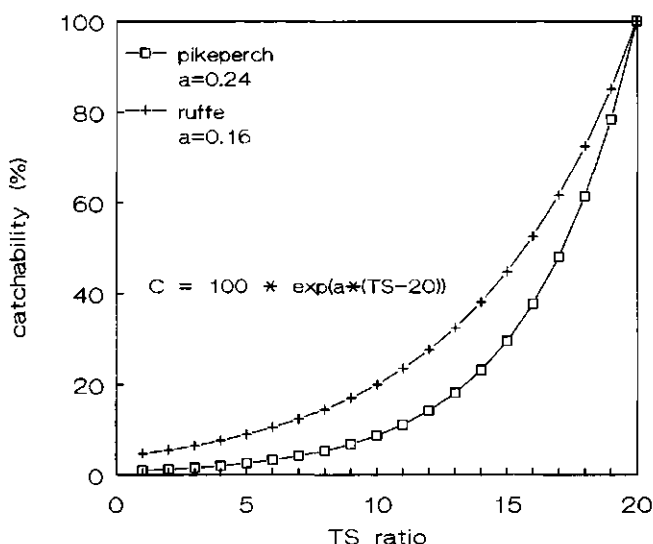


Fig. 4 Modelled relationship between light intensity, expressed as the total water depth: Secchi depth ratio (TS), and the catchability (C) of ruffe and age 0 pikeperch in Lake IJssel. A total water depth: Secchi depth of 20 was used as a reference point.

If the TS ratio is a good indication for the catchability then effects should be similar in both areas N and S. Significant effects of light intensity on catchability were found in both areas for ruffe, smelt, age 0 and 1 perch and age 0 pikeperch (Table 5). So for these species regression coefficients of fish catches on the TS ratio from both areas could be compared, using (3). To improve the estimates of the effect of light intensity on the catchability, data collected at area N in 1981-83 and at area S in 1983 were also used in this comparison (Table 6). For age 0 pikeperch and ruffe slopes did not differ significantly between the two areas. Therefore data could be combined to calculate an overall model for these two species. The negative effect of a higher light intensity near the bottom on the catchability was stronger for age 0 pikeperch than for ruffe (Table 6, Fig. 4). Catches of age 0 pikeperch decreased 22% and those of ruffe 15% as light intensity increased five-fold i.e. as the TS ratio is decreased by one unit. Slopes of the regression of the catches of both perch age-groups on light intensity differed significantly between the two areas studied (age 0: $p < 0.001$; age 1: $p < 0.01$). With the extended data set light intensity had no longer a significant effect on the catches of smelt.

The autumn trawl surveys aim to estimate YCS, in terms of age 0 abundance, of the commercially important pikeperch and perch. Log-transformed estimates of YCS of perch and pikeperch from the lake-wide trawl survey were highly

correlated with the log-transformed landings of the same year-classes by the commercial gill net fishery (perch: $r = 0.91$, $p < 0.01$ for the year-classes 1969-1984; pikeperch: $r = 0.69$, $p < 0.01$ for the year-classes 1971-1986) (unpublished data). Age 0 densities of perch and pikeperch are therefore regarded as good predictors of the yield. Since the effects of light intensity on catches of age 0 pikeperch are the strongest, uncorrected and corrected data of pikeperch were compared for their capability to predict landings. Data were corrected according to (4) using the mean TS ratio over the period 1966-1989 during the lake-wide survey as reference ratio ($TS_r = 13.1$). Corrected and uncorrected estimates of pikeperch YCS displayed the same fluctuations (Fig. 5). Corrected estimates varied from 98% lower (for 1968) to 349% higher (for 1988) than the uncorrected estimates. The correlations of corrected ($r = 0.61$; $p < 0.05$) and uncorrected ($r = 0.69$; $p < 0.01$) estimates, with the landings of the commercial gill net fishery for the year-classes 1971-86 were both significant, and regression coefficients were not significantly different from each other.

Table 6. Regression coefficients (A) and their standard error (S.E.) of linear models, $\log_e(C) = A \cdot TS$, to correct catch data (C) of four fish species for light intensity at the bottom, expressed as the total water depth: Secchi depth ratio (TS), for the two distinct areas N and S and lake-wide (L) in Lake IJssel. N = number of hauls; R^2 = fraction of variance explained; ** $p < 0.01$.

| SPECIES | AGE-GROUP | AREA | N | A | S.E. | R^2 |
|-----------|-----------|------|-----|-------|-------|--------|
| PERCH | 0 | N | 167 | 0.092 | 0.028 | 0.06** |
| PERCH | 0 | S | 41 | 0.459 | 0.075 | 0.49** |
| PERCH | 1 | N | 128 | 0.052 | 0.036 | 0.02 |
| PERCH | 1 | S | 41 | 0.246 | 0.051 | 0.38** |
| PIKEPERCH | 0 | N | 165 | 0.244 | 0.030 | 0.29** |
| PIKEPERCH | 0 | S | 38 | 0.243 | 0.089 | 0.17** |
| PIKEPERCH | 0 | L | 203 | 0.244 | 0.028 | 0.27** |
| RUFFE | ALL | N | 150 | 0.153 | 0.042 | 0.08** |
| RUFFE | ALL | S | 31 | 0.269 | 0.066 | 0.36** |
| RUFFE | ALL | L | 181 | 0.161 | 0.038 | 0.09** |
| SMELT | ALL | N | 151 | 0.021 | 0.027 | 0.00 |
| SMELT | ALL | S | 31 | 0.116 | 0.064 | 0.10 |

Catches without age 0 pikeperch became less frequent as the TS ratio increased (Fig. 6). In both surveys 45 out of 477 hauls caught no age 0 pikeperch. Of these 477 hauls 93 had a TS ratio ≤ 7 and 29 hauls out of the 45 with zero catches had a TS ratio ≤ 7 . Thus 4% of the catches with a TS ratio above 7 and 31% with a TS ratio equal to or below 7, caught no age 0 pikeperch.

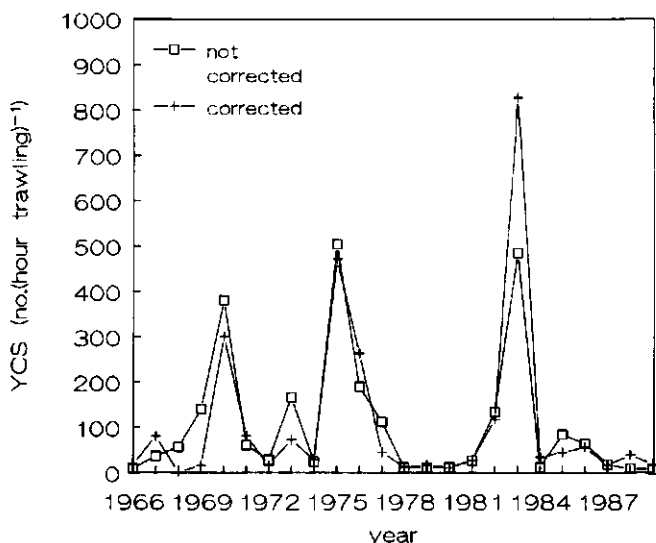


Fig. 5 Uncorrected and corrected pikeperch year-class strength estimates (YCS), indexed as mean number of age 0 fish per hour trawling during survey II in Lake IJssel, 1966-1989. Corrected = standardisation to the mean total water depth: Secchi depth (13.1) over this period for the effect of light intensity on the catchability.

DISCUSSION

Light intensity is an indicator of variation of catchability, and distance from shore an indicator of spatial variation in abundance of fish within the area investigated. For the lake-wide survey, only light intensity could be used to correct for variation in the catches. The effects of light intensity on catchability of pikeperch and ruffe could therefore be possibly overestimated. Thus equality of regression coefficients of light intensity for one species in one area was tested between estimates from the model based on light intensity data only and from the regression model, which also included distance from shore. For both species and both areas the regression coefficients from both models did not differ significantly. Therefore the model, which uses only light intensity as an independent variable, did not overestimate the effect of light intensity on the catchability of pikeperch and ruffe.

In this study catchability of fish is expressed as a function of light conditions near the bottom. The ratio (TS) between total water depth and Secchi disk reading was used as an index for these light conditions. In our study the TS ratio varied mainly between 6 and 15. The daily total incoming visible radiation on a standard clear day is $3.93 \cdot 10^6 \text{ J.m}^{-2}$ (Goudriaan and van Laar 1978) at

52°45' on November 1st, which corresponds with 2.83×10^4 lx. Average transmission in The Netherlands is about 50%. So light conditions at the bottom of Lake IJssel varied between 9×10^{-1} and 4.6×10^{-7} lx. Photographic studies on fish in the waters around Orkney, U.K., show that the ordered pattern of reaction behaviour to an approaching net, seen at high light levels ($> 10^{-3}$ lx), ceased at low light levels ($< 10^{-6}$ lx) (Glass and Wardle 1989). Although visual performance of the fish species in our study is not known, probably they are better capable in detecting the trawl at a TS ratio of 6 than of 15.

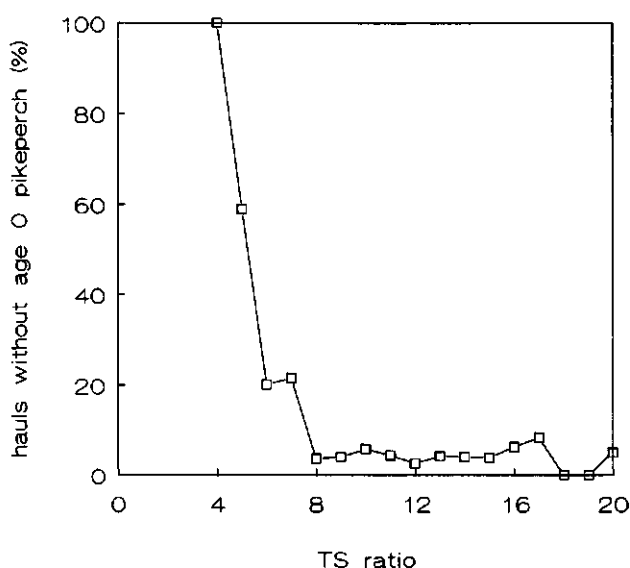


Fig. 6 Percent of trawl hauls without age 0 pikeperch vs total water depth: Secchi depth ratio (TS). Data of survey I and II combined. TS ratio 20 represents all hauls with TS ratio ≥ 20 . N = 477.

The effect of the TS ratio on the catchability of pikeperch and ruffe was similar in areas N and S, which have different depths. The TS ratio may therefore be a general indication of the catchability of these bottom dwelling species (Eloranta and Eloranta 1978; Nilsson 1979). The effects of the light conditions at the bottom on the catchability of all species were consistently stronger (but never significant, except for perch) in the more shallow area S than in area N. This difference is thought to be due not to the difference in light intensity, but to the noise of the survey vessel. This effect was more pronounced in shallow water and under calm weather conditions.

Temperature influences catchability via the swimming performance of fishes (Wardle 1983). Possible differences in catchability between years caused by

temperature were not analysed, because data were corrected for within-year mean abundance. The maximum variation in water temperatures recorded during a survey was 2.6°C in 1981. Thus within-year differences in swimming performance probably do not differ much.

Increased light intensity had a negative effect on the catchability of all species. This effect was strongest for pikeperch and then ruffe. Effects for perch, which were of similar magnitude to those for ruffe, were not consistent for both areas. Perhaps a more patchy distribution of perch than those of the other species results in a higher variation in the catches. Schooling behaviour and water clarity are highly correlated for yellow perch in Lake Mendota; at higher water clarity the space used by a school is larger because of improved visibility (Hergenrader and Hasler 1968). Data of Nielsen (1983) were recalculated to compare the effect of light intensity on the catchability of yellow perch in Oneida Lake with the effects found for perch in Lake IJssel. Light intensity had a stronger effect (regression coefficient = 0.48) in Oneida Lake than in Lake IJssel, perhaps because the absolute light intensity near the bottom was much higher in Oneida Lake.

The effect of light intensity on the catchability of smelt could not be quantified. Correlations between the catches of smelt and light intensity were significant for the years 1984-88, but including data from 1981-83 resulted in an insignificant correlation. Probably the vertical migration of smelt in relation to variable light conditions, following their zooplankton food (Dembinski 1971; Nilsson 1979; Northcote and Rundberg 1970), induces an extra source of variation in smelt catches with bottom trawls. Hydroacoustic surveys should be made simultaneously with a trawl sampling programme to register the vertical distribution of the smelt (Burczynski et al. 1987).

The effect of differences in catchability on the estimates of relative YCS of pikeperch over the period 1966 - 1989 is small. This is partly explained from the initial sampling strategy which was to wait for favourable conditions, resulting in small variations in water clarity during surveys. Further, YCS variation for pikeperch in Lake IJssel is so large that it overrides the effects of changes in catchability. However, the changes in catchability from one year to another can lead to serious over- or underestimation of the survival rate of a year-class.

Age 0 pikeperch catches were the most susceptible to changes in water clarity. Zero catches of age 0 pikeperch were mainly due to low catchability, not to low abundance. Because zero catches cannot be standardised for light intensity, they have to be minimised. Therefore, sampling can be optimised by interrupting the programme when water clarity exceeds a certain level and by standardizing catches to a reference TS ratio for all non-zero hauls. Our results give an objective means for deciding what fraction of zero values is acceptable.

In Lake IJssel, the TS ratio can vary between 2 and 40 (Willemsen 1977). Large variations in water clarity are also found in other situations. In the Oster Lakes (Federal Republic of Germany), Secchi depths vary between 0.5 and 8 m, which results in a TS ratio of 3.9 and 62 respectively, when related to maximum water depth (Bohl 1980). Mean Secchi depth readings in Oneida Lake varied between 1.6 and 3.9 m, and this corresponds with TS ratios of 1.7 and 4.2 when related to mean water depth (Nielsen 1983).

Differences in light conditions and thus differences in catchability will always be found when samples are taken simultaneously at different depths in the water column. Therefore, conclusions that fish is vertically distributed as determined by trawling at different depths or vertical gill netting, can only be justified provided that experimental studies (Scherer 1976) and echo sounding studies (e.g. Dembinski 1971; Kelso et al. 1974; Northcote and Rundberg 1970; Robinson and Barraclough 1978) prove that vertical positioning of fish is related to light intensity.

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REFERENCES

- Atkinson, D. B. 1989. Diel movements of beaked redbait and the implications of these for stratified random bottom trawl estimates of biomass and abundance. *N. Am. J. Fish. Manag.* 9: 163-170.
- Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia* 44: 368-375.
- Burczynski, J. J., P. H. Michaletz, and G. M. Marrone. 1987. Hydroacoustic assessment of the abundance and distribution of rainbow smelt in Lake Oahe. *N. Am. J. Fish. Manag.* 7: 106-116.
- Butterworth, A. J., and T. F. Coles. 1977. The use of a midwater trawl to sample lacustrine fish populations. *Fish. Manag.* 8: 35-42.
- Carper, G. L., and R. W. Bachmann. 1984. Wind resuspension of sediments in a prairie lake. *Can. J. Fish. Aquat. Sci.* 41: 1763-1767.
- Dembinski, W. 1971. Vertical distribution of vendace, *Coregonus albula* L., and other pelagic fish species in some Polish lakes. *J. Fish Biol.* 3: 341-357.
- Eloranta, P., and A. Eloranta. 1978. Vertical distribution of fishes in one lake deep (Lake Kuusvesi, Central Finland). *Verh. Intern. Verein. Limnol.* 20: 2092-2097.

- Glass, C. W., and C. S. Wardle. 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. *Fish. Res.* 7: 249-266.
- Goudriaan, J., and H. H. van Laar. 1978. Calculation of daily totals of the gross CO₂ assimilation of leaf canopies. *Neth. J. agric. Sci.* 26: 373-382.
- Hergenrader, G. L., and A. D. Hasler. 1968. Influence of changing seasons on schooling behavior of yellow perch. *J. Fish. Res. Board Can.* 25: 711-716.
- Kelso, J. R. M., E. E. Pickett, and R. G. Dowd. 1974. A digital echo-counting system used in determining abundance of freshwater pelagic fish in relation to depth. *J. Fish. Res. Board Can.* 31: 1101-1104.
- Lorenzen, M. W. 1980. Use of chlorophyll-Secchi disk relationships. *Limnol. Oceanogr.* 25: 371-372.
- Nielsen, L. A. 1983. Variation in the catchability of yellow perch in an otter trawl. *Trans. Am. Fish. Soc.* 112: 53-59.
- Nilsson, N. 1979. Food and habitat of the fish community of the offshore region of Lake Vänern, Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 58: 126-139.
- Northcote, T. G., and H. Rundberg. 1970. Spatial distribution of pelagic fishes in Lambarfjärden (Mälaren, Sweden) with particular reference to interaction between *Coregonus albula* and *Osmerus eperlanus*. *Rep. Inst. Freshw. Res. Drottningholm* 50: 133-167.
- Pennington, M. 1983. Efficient estimators of abundance, for fish and plankton surveys. *Biometrics* 39: 281-286.
- Quinn, N. J., and B. L. Kojis. 1987. The influence of diel cycle, tidal direction and trawl alignment on beam trawl catches in an equatorial estuary. *Env. Biol. Fish.* 19: 297-308.
- Robinson, D. G., and W. E. Barraclough. 1978. Population estimates of sockeye salmon (*Oncorhynchus nerka*) in a fertilized oligotrophic lake. *J. Fish. Res. Board Can.* 35: 851-860.
- Scherer, E. 1976. Overhead-light intensity and vertical positioning of the walleye, *Stizostedion vitreum vitreum*. *J. Fish. Res. Board Can.* 33: 289-292.
- Sissenwine, M. P., T. R. Azarovitz, and J. B. Suomala. 1983. Determining the abundance of fish. p. 51-101. *In* A. G. MacDonald and I. G. Priede [eds.] *Experimental biology at sea*. Academic Press, London.
- Wardle, C. S. 1983. Fish reactions to towed fishing gears, p. 167-195. *In* A.G. MacDonald and I.G. Priede [eds.] *Experimental biology at sea*. Academic Press, London.
- Willemsen, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. *J. Fish. Res. Board Can.* 34: 1710-1719.

Chapter 3

YEAR-CLASS STRENGTH OF EURASIAN PERCH (*PERCA FLUVIATILIS* L.) AND PIKEPERCH (*STIZOSTEDION LUCIOPERCA* (L.)) IN RELATION TO STOCK SIZE, WATER TEMPERATURE AND WIND IN LAKE IJssel, THE NETHERLANDS, 1966-1989.

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ABSTRACT

Recruitment, indexed as the age 0 abundance in bottom trawls, of Eurasian perch (*Perca fluviatilis*) varied 400-fold and of pikeperch (*Stizostedion lucioperca*) 70-fold over the period 1966-89. Hypotheses were formulated on the possible relationship between recruitment and stock biomass, prey fish availability, water temperature and wind velocity. For perch 36% to 71% of the variation in recruitment could be explained by stock biomass of piscivores, water temperature, and year of sampling; for pikeperch 38% to 86% could be explained by water temperature, wind velocity and year of sampling. For both species strong year-classes were favoured by high summer temperatures and by low temperatures in April; a late increase in water temperature during spring, probably resulting in postponed spawning, favoured recruitment. Stock-recruitment relationships could not be demonstrated. The impact of the commercial fishery, which possibly accounted for the significant correlation between year of sampling and year-class strength, and of fish-eating birds might have clouded interactions among fish species. Year-class strength variation of *Perca* spp. in Lake IJssel was higher than those described for other water bodies, while for *Stizostedion* spp. it fell within the observed range. Implications for future research and management are discussed.

INTRODUCTION

Year-class strengths (YCS) of percids vary highly. Koonce et al. (1977) gave an overview of year-class strength variation (YCSV) and possible explanatory factors. Positive factors mentioned are a large parental stock size (Henderson and Nepszy 1988), a fast rate of spring warming (Busch et al. 1975), high water temperatures (Clady 1976, Willemsen 1977), high water levels (Henderson 1985; Kallemeyn 1987), a large abundance of alternative prey buffering cannibalism (Forney 1974) and an early onset of piscivory (Buijse and Houthuijzen 1992; Van Densen 1985), while negative factors include strong winds (Clady 1976; Clady and Hutchinson 1975), intensive predation and cannibalism (Alm 1952; Chevalier 1973; Forney 1971; LeCren 1987; Mills and Hurley 1990; Nielsen 1980; Staub and Krämer 1991; Tarby 1974), large variations in water temperature (Serns 1982), ice cover during the previous winter (Kipling 1976), and acidification (Raitaniemi et al. 1988; Rask and Tuunainen 1990). Because detailed information on survival of age 0 percids in Lake IJssel were not available, possible factors influencing year-class formation were selected from the literature on percids, particularly from the detailed studies in Oneida Lake (N.Y.), USA (Chevalier 1973; Clady 1976; Forney 1971, 1974, 1977, 1976, 1980; Mills and Forney 1988; Mills et al. 1987; Nielsen 1980; Tarby 1974) and in Windermere, UK (Craig and Kipling 1983; Craig et al. 1979; Guma'a 1978; Kipling 1976; LeCren 1987; LeCren et al. 1977; Mills and Hurley 1990).

Willemsen (1977) estimated YCS of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in Lake IJssel at three life stages: at the larval stage, as age 0 fish in November and when adult as the accumulated catch in the commercial fishery. In his 10-years time series (1966-1975), larval and age 0 abundance were not correlated with each other, while age 0 abundance and accumulated catch were, suggesting that the YCS is determined by the end of the first year of life. Age 0 abundance of pikeperch was positively correlated with the sum of degree days over 14°C, but possible explanatory mechanisms were not identified.

Perch and pikeperch are the most important predators in Lake IJssel. Pikeperch becomes piscivorous at age 0, while perch switches towards piscivory at age 1 to 3. European smelt (*Osmerus eperlanus*) is the most important food item for perch and age 0 pikeperch (Buijse and Van Densen 000; Buijse and Houthuijzen 1992; Willemsen 1977). Willemsen (1983) suggested that cannibalism among pikeperch is rare due to the abundance of alternative fish prey as smelt and ruffe (*Gymnocephalus cernua*). For perch, it was shown that in a year with high abundance of age 0 perch cannibalism was more frequent, but age 0 smelt always was the more selected fish prey (Buijse and Van Densen

000). The onset of piscivory for age 0 pikeperch is a necessary condition to survive during the first year. Condition of the larger smelt-eating age 0 pikeperch increased from August to September, while the condition of the smaller zooplankton- or macrofauna-eating cohort members deteriorated over the same time span (Buijse and Houthuijzen 1992).

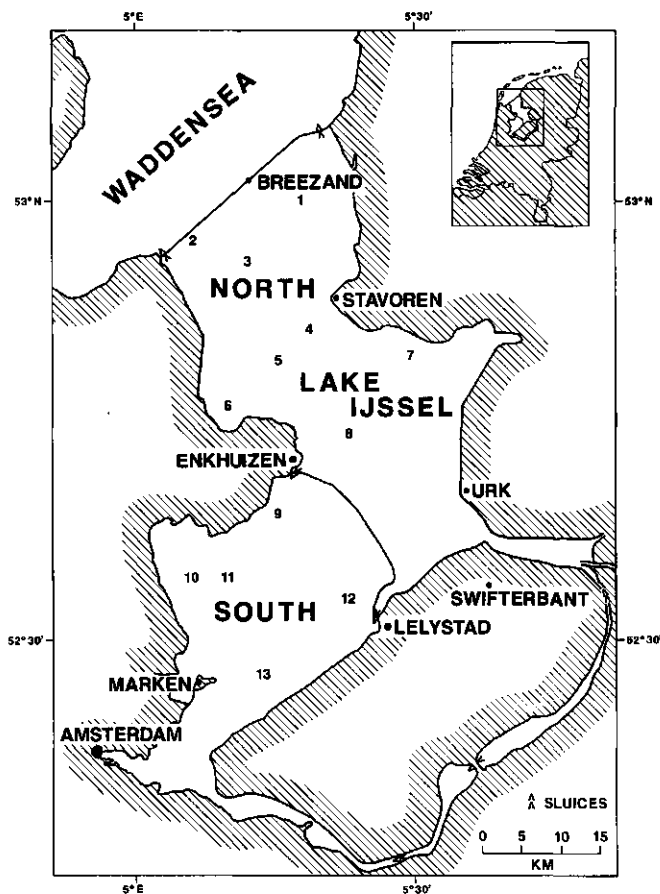


Fig. 1. Location of Lake IJssel and of the sampling sites (1 to 13) used during the trawl surveys. Water temperatures were measured daily at Marken, Enkhuzen, Urk, Stavoren and Breezand; wind velocity measurements were carried out at Swifterbant.

In Lake IJssel, both perch and pikeperch are exploited by a commercial gill net fishery. Variations in YCS induce strong variations in the annual yield per species. Especially for pikeperch the exploitation rate is high and most females are caught before maturation (Willemsen 1983). The possibility of recruitment

overfishing is particularly relevant in this case, because a stock-recruitment relationship bears considerable consequences on the effectiveness of different management strategies.

The aim of our study was to determine more precisely in which period during the first year of life YCS of perch and pikeperch are determined. This study includes a longer 24-years time series and evaluates more variables for their possible influence on YCS than the previous study by Willemsen (1977). With the variables selected (stock biomass, smelt availability, water temperature and wind velocity) a stepwise multiple regression analysis was carried out to investigate which factors contributed significantly to the year-class formation of perch and pikeperch in Lake IJssel. From 1987-1989 research has been focussed on the dynamics of age 0 percids, and the outcomes are used to discuss the conclusions of the regression analysis. The YCSV of percids in Lake IJssel are compared with reported variations observed in other systems. The shortcomings of our study and the consequences for further research and management are discussed.

MATERIAL AND METHODS

Study area

Lake IJssel (52°45'N, 5°20'E) is a 182,000 ha shallow eutrophic water body, that is highly exposed to wind action. The lake has been divided into a northern basin (112,000 ha) and a southern basin (70,000 ha) by the construction of a dyke in 1975 (Fig. 1). The northern basin has an average depth of 4.5 m, with depressions down to 10 m deep caused by former tidal currents. The southern basin has an average depth of 3.6 m. A more detailed description of the study area is given by Buijse and Van Densen (000). An attempt was made by Buijse et al. (1991) to quantify the major routes for energy transfer in the food web. The most common fish species are eel (*Anguilla anguilla*), smelt, the cyprinids bream (*Abramis brama*) and roach (*Rutilus rutilus*) and the percids perch, pikeperch and ruffe. The smelt stock consists of a short-lived (mainly two age-groups) land-locked population together with a much smaller population of migratory smelt. There is a commercial fishery for pikeperch and perch with gill nets (101 mm stretched mesh), for eel with fyke nets, eel boxes and long lines, and for spawning smelt with fyke nets (Van Densen et al. 1990). The gill net fishery is open from July 1 until March 15, but is practised predominately in autumn and winter. Minimum legal landing sizes of perch and pikeperch are 22 and 42 cm, respectively.

Collection of fish

Fish were caught with a bottom trawl at eight sampling sites in the northern and five in the southern part of Lake IJssel in the period 1966-1989 (Fig. 1). Depth at the sampling sites varied from 2.5 to 9.5 m. The stations were fished during daytime in August and November. A description of the trawl is given by Buijse et al. (1992). Haul duration varied from 10 to 45 min. All catches were standardised to 10 min fishing corresponding to a swept area of about 0.8 ha. From 1987 to 1989 sampling was also conducted at the end of June and in September (Buijse and Van Densen 000). This latter portion of the study thus comprised only three years and was considered only as exploratory.

All fish were sorted by species, weighed, and if necessary subsampled. Individual fish were measured to the nearest cm total length. Methods and results of food studies of perch are described in Buijse and Van Densen (000).

Market sampling to estimate size and age structure of the commercial landings has been carried out since 1968 for pikeperch and since 1970 for perch. Samples were taken on one to seven occasions during the gill net fishing season (September to March). Length was measured to the nearest cm total length. Scales and fin rays were collected for age determination irrespective of sex. The origin of the gill net catches could not be ascertained, because gill nets are sometimes set by one boat on both sides of the dyke separating the lake and answers from the fishermen about the origin of the catch appeared not to be reliable. Therefore, catches from the northern and southern part of the lake had to be combined in the analysis.

Recruitment indices

Estimates of YCS during the first year of life are available from the November surveys for all years. Except for 1974 and the years 1984-1986, an additional estimate is also available from the August survey. An index of recruitment was calculated for the northern and the southern part separately by taking the geometric mean of the catches (adding 1). Age 0 and older fish could be readily identified from the length frequency distributions, because there was no overlap between the young-of-the-year and the older fish. The unweighted mean of the abundances in the northern and southern part was considered a representative index of YCS for the whole of Lake IJssel. Year-classes are indicated in the text with square brackets [].

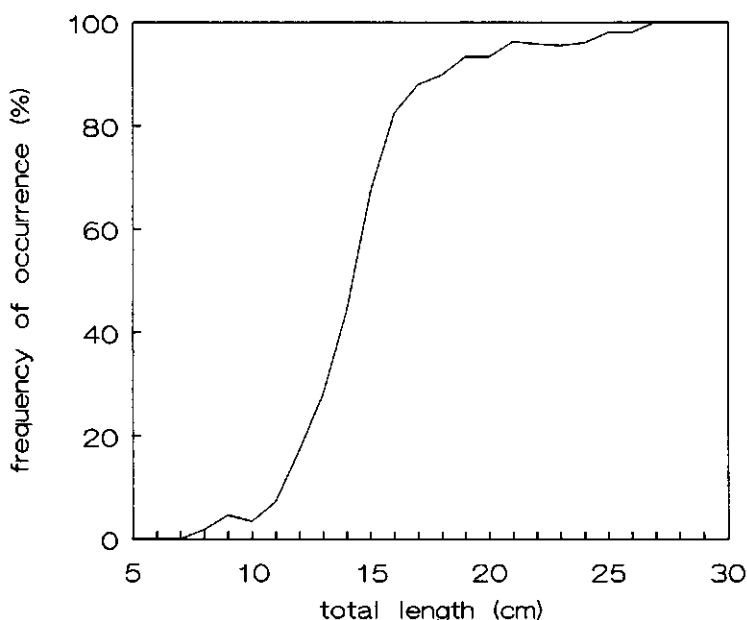


Fig. 2. Percentage of perch which were piscivorous per length-class. Data are based on 10,388 6-34 cm perch originating from trawl samples in June, August and September 1987-1989 (Buijse and Van Densen 000).

Spawning and predator stock biomass

Cohort analyses (Jones 1984) of the commercial landings were carried out to estimate stock biomass of the two species. The range of year-classes included [67] to [86] of pikeperch and [69] to [85] of perch. Length frequencies of the market samples were split into age-groups based on age-length keys. The estimated landings per year and year-class are listed in Appendix 1 and 2. Varying input values of the annual instantaneous fishing mortality rate (F) and the instantaneous natural mortality rate (M) were used for a convergence check. Although these input values influenced the absolute estimates of stock biomass, correlations between estimates were highly significant ($p < 0.01$). The influence of the input values on the estimation of stock biomass, which biomass is needed to investigate stock-recruitment relationship, was therefore considered negligible. Consequently, input values were chosen for both species resulting in F -values: for pikeperch 0.4 for age 5 and older and for perch 0.8 for the age 7 and older. A value of 0.2 was assumed for M in both species. For the age-groups in the more recent years, the terminal F -value was based on the mean F in the same age-group estimated for preceding year-classes.

The total stock biomass was estimated from the stock sizes by age-group, mean length at age and a length-weight relationship ($W = 0.0059 * L^{3.11}$ and

$W = 0.0104 * L^{3.13}$ for pikeperch and perch respectively, total weight W in g and total length L in cm).

The female spawning stock biomass was estimated on April 1 by assuming a 1:1 sex ratio and age 2, 3, and 4 female pikeperch (Willemsen 1977) as well as perch (unpublished data) being 0, 50 and 100% mature.

The stock biomass of piscivorous perch and pikeperch was estimated from observations on the frequency of occurrence of piscivory. Although age 0 pikeperch and in some years age 1 perch were piscivorous, these predator age-groups prey almost exclusively on age 0 smelt (Buijse and Van Densen 000; Willemsen 1977). Since we are mainly concerned here with predation on perch and pikeperch, all age 1 and older pikeperch and all age 2 and older perch were considered potential predators. The stock biomass of piscivores was calculated on October 1. Based on trawl surveys for perch it was also possible to specify the piscivorous stock biomass per lake part. The frequency of occurrence of fish in stomachs by size-class as observed during trawl surveys from 1987 to 1989 was used to estimate the stock biomass of piscivorous perch (Fig. 2). Age 1 and older pikeperch are seldom caught in survey trawls. Thus their biomass could not be specified per lake part.

Alternative fish prey

Food studies have shown that age 0 perch is preyed upon by both species, while age 0 pikeperch was found only once in 10,388 perch stomachs and was therefore assumed to be preyed upon only by pikeperch (Buijse and Van Densen 000; Willemsen 1977). For adult perch, smelt serves as an alternative fish prey and when abundant might buffer predation on age 0 perch (Buijse and Van Densen 000). In pikeperch, the onset of piscivory required for survival is enhanced by a high availability of smelt (high abundance and small size) (Buijse and Houthuijzen 1992; Van Densen 1985). Smelt availability was therefore characterised by its total biomass and the mean length of age 0 fish. The abundance of smelt was recorded during the same surveys used for the indices of YCS of the percids. An index of biomass was calculated by taking the geometric mean of the weights of the catches for the two lake parts separately. The total lake index was based on the unweighted means of these two.

Wind

Since wind stress is supposed to influence survival only in the egg and larval stage (Clady 1976), the average wind velocity during the first 4 weeks after spawning was calculated as a potential factor influencing YCS. Although actual observations on the timing of spawning were not available for Lake IJssel,

Willemsen (1977) indicates that perch spawn between 8°C and 12°C, and pikeperch between 11°C and 15°C. Therefore, the spawning date was assumed to be the day when the temperature exceeded 8°C for perch and 11°C for pikeperch. Wind velocity has been measured daily since 1973 at 9:00 MET at 2 m height at a meteorological station close to the lake (Fig. 1). Fluctuations in water level have also been mentioned as a year-class determining factor, because they may cause variations in spawning habitat (Kallemeyn 1987). Since the water level in Lake IJssel hardly fluctuates, variation in spawning habitat are most probably negligible. Still, short-term variations up to 0.5 m induced by wind action may occur. Since perch spawn mostly at depths of 0.5 - 3 m in natural lakes (Thorpe 1977 p. 23), periods of strong winds during egg incubation could also have a negative effect on recruitment by temporarily altering the water level at the littoral spawning sites.

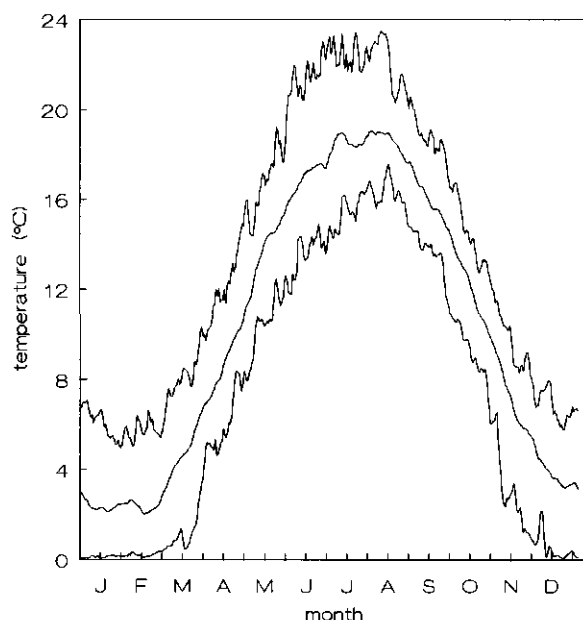


Fig. 3. The minimum, mean and maximum daily water temperature (°C) in Lake IJssel during the period 1966 - 1989.

Water temperature

Water temperatures have been measured daily at 9:00 MET at five sites (Fig. 1). Since water temperatures did not differ significantly between the northern (4 sites) and southern part (1 site), they have been averaged for the entire lake.

The average annual temperature cycle with the minimum and maximum values are given in Fig. 3. The maximum daily water temperature over the

period 1966 - 1989 was 23.5°C. Since the mechanism behind a possible relation between recruitment and temperature is not known, the annual temperature regime has been characterised in several ways: (1) the spawning date, defined as the day when the water temperature exceeded the minimum value required for spawning (see above), (2) warming rate (Henderson and Nepszy 1988; Serns 1982) and standard deviation of the warming rate during the period from the spawning date until June 21, (3) mean monthly temperatures in April, May and June, mean temperatures during the period July - August, and (4) the yearly sum of degree days over 14°C (LeCren 1987).

Recruitment models

The stock-recruitment relationship for percids is probably best described by a Ricker-curve (Ricker 1975 p. 282), because both species are as well producers as consumers of their own offspring.

$$R = \alpha B_s e^{-\beta B_p}$$

where:

- R = number of recruits
- α = a dimensionless parameter
- β = a parameter with dimensions of 1/B
- B_s = spawning stock biomass (kg.ha⁻¹)
- B_p = piscivorous stock biomass (kg.ha⁻¹)

The log_e of the number of recruits is used as dependent variable, because effects are expected to act multiplicative. The potential influence of various abiotic and biotic factors on age 0 YCS in August and November, and on the mortality from August to November was evaluated. Three types of models were tested with forward stepwise multiple regression. Firstly, models which explained recruitment in August and November were tested using the combined recruitment indices for the entire lake. These models used the following independent variables:

$$\log_e R_{\text{perch}} = f(\text{water temperature, wind velocity, log}_e \text{ spawning stock biomass of perch, stock biomass of piscivorous perch and pikeperch}^1, \text{ smelt biomass, year})$$

$$\log_e R_{\text{pikeperch}} = f(\text{water temperature, wind velocity, } \log_e \text{ spawning stock biomass of pikeperch, stock biomass of piscivorous pikeperch}^{1}), \text{ smelt biomass, age 0 smelt length, year})$$

¹⁾based on cohort analysis

Secondly, models which explained age 0 recruitment in August and November were tested separately for the northern and the southern part. Splitting the data set into a separate set for both the northern and the southern part might supply additional information, because both lake parts differ only in the biotic factors and not in water temperature or wind velocity. These models used the following independent variables:

$$\log_e R_{\text{perch}} = f(\text{water temperature, wind velocity, stock biomass of piscivorous perch}^{2}), \text{ smelt biomass, year})$$

$$\log_e R_{\text{pikeperch}} = f(\text{water temperature, wind velocity, smelt biomass, age 0 smelt length, year})$$

²⁾based on surveys

Thirdly, models using only biotic factors (biomass of predator and alternative fish prey) were tested to explain mortality from August to November. These models also used combined data of both lake parts. Mortality (M) was estimated by taking the $\log_e R_{\text{August}} - \log_e R_{\text{November}}$. The following models were tested:

$$M_{\text{perch}} = f(\text{stock biomass of piscivorous perch and pikeperch}^{1}), \text{ smelt biomass, year})$$

$$M_{\text{pikeperch}} = f(\text{stock biomass of piscivorous pikeperch}^{1}), \text{ smelt biomass, age 0 smelt length, year})$$

Only those explanatory variables that were significant at $P < 0.05$ were included in the models.

Table 1. Number of sampling sites, age 0 abundance of pikeperch and perch, biomass of smelt, total length of age 0 smelt, piscivorous stock biomass (psb) of perch (based on trawl surveys), psb and spawning stock biomass (ssb) of perch and pikeperch (based on cohort analysis of the landings from the commercial gill net fishery) and water temperature in and wind velocity at the northern (N) and southern (S) part of Lake IJssel from 1966 to 1989. dd14 = sum of degree days above 14°C; dano8, dano11 = date when the water temperature exceeded 8°C and 11°C; roi8, roi11 = warming rate of the water temperature in the period from dano8 or dano11 to June 21; sd8, sd11 = standard deviation of the warming rate roi8 or roi11; wind8, wind11 = mean wind velocity in a 4-weeks period after dano8 or dano11; c.v. = coefficient of variation; blanks are missing data.

| month | number of sampling sites | | | | pike age 0 | | pike age 0 | | pike age 0 | | perch age 0 | | perch age 0 | | perch age 0 | | perch age 0 | | smelt biom | smelt biom | smelt biom | smelt biom | smelt leng | smelt leng |
|----------|--------------------------|-----|-----|-----|------------|-----|------------|-----|------------|------|-------------|-----|-------------|------|-------------|------|-------------|-----|------------|------------|------------|------------|------------|------------|
| | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov | aug | nov |
| year | S | S | N | N | S | N | S | N | S | N | S | N | S | N | S | N | S | N | S | N | S | N | cm | cm |
| 66 | 2 | 2 | 7 | 4 | 38 | 1 | 2 | 1 | 1 | 0 | 2 | 6 | 3.3 | 8.4 | 6.9 | 5.7 | 6.9 | 7.0 | | | | | | |
| 67 | 2 | 2 | 7 | 4 | 6 | 0 | 10 | 2 | 0 | 0 | 0 | 3 | 4.1 | 3.2 | 8.5 | 5.4 | 6.8 | 6.5 | | | | | | |
| 68 | 1 | 1 | 5 | 3 | 0 | 0 | 18 | 1 | 2 | 1 | 3 | 3 | 3.5 | 2.4 | 6.3 | 9.2 | 6.8 | 6.9 | | | | | | |
| 69 | 2 | 2 | 5 | 7 | 113 | 7 | 35 | 12 | 69 | 15 | 255 | 98 | 0.9 | 2.5 | 16.5 | 10.1 | | | | | | | | |
| 70 | 3 | 3 | 4 | 6 | 10 | 22 | 67 | 60 | 15 | 11 | 251 | 169 | 2.0 | 0.6 | 5.2 | 6.2 | 6.0 | 6.6 | | | | | | |
| 71 | 4 | 5 | 4 | 8 | 31 | 25 | 15 | 5 | 21 | 29 | 84 | 155 | 0.7 | 0.8 | 6.7 | 6.9 | 6.2 | 6.5 | | | | | | |
| 72 | 4 | 4 | 5 | 8 | 4 | 0 | 5 | 4 | 0 | 0 | 2 | 3 | 7.4 | 13.7 | 8.6 | 11.5 | 6.4 | 7.1 | | | | | | |
| 73 | 4 | 5 | 3 | 7 | 48 | 25 | 20 | 35 | 34 | 18 | 22 | 136 | 18.9 | 28.1 | 12.0 | 25.4 | 7.3 | 7.2 | | | | | | |
| 74 | 4 | 4 | 8 | | | | 7 | 1 | | | 32 | 0 | | | 20.8 | 36.0 | 7.0 | 7.4 | | | | | | |
| 75 | 2 | 4 | 6 | 8 | 64 | 6 | 91 | 77 | 99 | 21 | 393 | 621 | 3.1 | 6.9 | 11.9 | 10.8 | 6.9 | 6.8 | | | | | | |
| 76 | 2 | 3 | 6 | 7 | 13 | 4 | 18 | 45 | 27 | 93 | 146 | 221 | 3.2 | 2.2 | 5.8 | 15.7 | 6.0 | 8.5 | | | | | | |
| 77 | 2 | 5 | 3 | 8 | 8 | 2 | 32 | 5 | 49 | 1 | 42 | 4 | 2.9 | 2.8 | 2.1 | 4.2 | 6.1 | 6.7 | | | | | | |
| 78 | 2 | 5 | 5 | 8 | 30 | 13 | 2 | 2 | 96 | 36 | 1286 | 74 | 21.5 | 0.3 | 4.7 | 5.3 | 6.9 | 8.3 | | | | | | |
| 79 | 5 | 5 | 7 | 8 | 5 | 5 | 1 | 2 | 2 | 4 | 8 | 29 | 8.9 | 0.8 | 18.2 | 23.6 | 6.1 | 7.4 | | | | | | |
| 80 | 4 | 5 | 8 | 7 | 7 | 2 | 1 | 3 | 11 | 7 | 96 | 122 | 3.4 | 12.9 | 19.9 | 15.5 | 7.0 | 7.3 | | | | | | |
| 81 | 4 | 5 | 7 | 8 | 2 | 7 | 4 | 5 | 3 | 1 | 6 | 4 | 6.2 | 23.5 | 9.8 | 14.5 | 6.8 | 8.1 | | | | | | |
| 82 | 5 | 4 | 8 | 8 | 62 | 19 | 12 | 33 | 234 | 11 | 354 | 40 | 11.7 | 17.5 | 8.8 | 11.6 | 6.7 | 7.4 | | | | | | |
| 83 | 3 | 5 | 8 | 6 | 2 | 15 | 11 | 150 | 52 | 41 | 187 | 115 | 1.6 | 7.1 | | 10.5 | 21.7 | 6.5 | 7.2 | | | | | |
| 84 | | 5 | | 8 | | | 1 | 3 | | | 33 | 26 | | | 5.9 | 21.0 | 6.7 | 7.3 | | | | | | |
| 85 | | 5 | | 8 | | | 20 | 8 | | | 71 | 775 | | | 6.4 | 12.3 | 6.5 | 6.6 | | | | | | |
| 86 | | 5 | | 8 | | | 11 | 11 | | | 385 | 303 | | | 5.5 | 13.1 | 6.6 | 7.3 | | | | | | |
| 87 | 5 | 5 | 8 | 8 | 0 | 4 | 6 | 0 | 2 | 62 | 18 | 16 | 0.4 | 15.6 | 15.3 | 7.6 | 6.5 | 7.3 | | | | | | |
| 88 | 5 | 5 | 8 | 8 | 1 | 4 | 0 | 3 | 16 | 10 | 5 | 17 | 4.5 | 5.6 | 2.5 | 8.4 | 6.0 | 6.7 | | | | | | |
| 89 | 5 | 5 | 8 | 8 | 3 | 30 | 0 | 2 | 112 | 1049 | 41 | 207 | 2.5 | 6.1 | 1.9 | 11.6 | 7.5 | 8.2 | | | | | | |
| mean | | | | | 22 | 10 | 16 | 20 | 42 | 70 | 155 | 131 | 5.5 | 8.1 | 9.2 | 13.0 | 6.6 | 7.2 | | | | | | |
| c.v. (%) | | | | | 130 | 98 | 131 | 174 | 133 | 320 | 172 | 146 | 101 | 97 | 58 | 58 | 6 | 8 | | | | | | |
| minimum | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 | 0.3 | 1.9 | 4.2 | 6.0 | 6.5 | | | | | | |
| maximum | | | | | 113 | 30 | 91 | 150 | 234 | 1049 | 1286 | 775 | 21.5 | 28.1 | 20.8 | 36.0 | 7.5 | 8.5 | | | | | | |

1) no.(10 min trawling)⁻¹

2) kg.(10 min trawling)⁻¹

3) kg.ha⁻¹

4) °C.d⁻¹

5) m.s⁻¹

Table 1 continued.

| year | perch psb nov S 2) | perch psb nov N 2) | perch ssb 3) | perch ssb 3) | perch psb 3) | perch psb 3) | apr °C | may °C | jun °C | julaug °C | dd14 °C.d | dano8 10-Apr | dano11 29-Apr | roi8 4) | sd8 4) | roi11 4) | sd11 4) | wind8 wi 5) |
|----------|--------------------------------|--------------------------------|--------------------|--------------------|--------------------|--------------------|-----------|-----------|-----------|--------------|--------------|-----------------|------------------|------------|-----------|-------------|------------|----------------|
| 66 | 0.4 | 1.6 | | | | | 7.7 | 15.1 | 18.3 | 17.4 | 428 | 10-Apr | 29-Apr | 0.14 | 0.59 | 0.14 | 0.57 | |
| 67 | 1.7 | 1.6 | | | | | 8.5 | 14.1 | 16.5 | 19.2 | 481 | 13-Apr | 01-May | 0.11 | 0.43 | 0.11 | 0.49 | |
| 68 | 2.1 | 1.1 | | | | | 9.6 | 12.6 | 17.1 | 18.2 | 432 | 28-Mar | 19-Apr | 0.12 | 0.41 | 0.11 | 0.36 | |
| 69 | 0.9 | 1.2 | | | | | 7.8 | 13.7 | 17.0 | 19.8 | 550 | 08-Apr | 03-May | 0.14 | 0.52 | 0.13 | 0.55 | |
| 70 | 4.3 | 4.4 | | | | 3.6 | 7.5 | 13.9 | 18.8 | 18.1 | 473 | 17-Apr | 06-May | 0.18 | 0.55 | 0.18 | 0.60 | |
| 71 | 5.5 | 7.5 | | | | 8.4 | 8.7 | 14.4 | 16.3 | 19.1 | 477 | 11-Apr | 04-May | 0.08 | 0.39 | 0.06 | 0.42 | |
| 72 | 5.7 | 7.1 | | 0.18 | | 6.3 | 8.6 | 13.0 | 15.5 | 18.5 | 361 | 03-Apr | 04-May | 0.09 | 0.45 | 0.08 | 0.50 | |
| 73 | 9.2 | 14.1 | 1.3 | 0.36 | 8.8 | 4.0 | 7.9 | 13.1 | 17.5 | 19.2 | 527 | 27-Mar | 04-May | 0.13 | 0.36 | 0.17 | 0.40 | 6.0 |
| 74 | 7.4 | 12.7 | 2.5 | 0.18 | 9.4 | 4.1 | 10.2 | 13.4 | 16.7 | 17.9 | 386 | 29-Mar | 09-Apr | 0.12 | 0.46 | 0.10 | 0.48 | 4.3 |
| 75 | 6.2 | 21.3 | 2.7 | 0.13 | 8.9 | 6.9 | 7.7 | 12.8 | 16.6 | 20.0 | 555 | 19-Apr | 29-Apr | 0.17 | 0.41 | 0.14 | 0.42 | 4.5 |
| 76 | 12.3 | 5.1 | 2.2 | 0.34 | 7.1 | 4.3 | 9.1 | 13.9 | 18.2 | 19.9 | 567 | 11-Apr | 07-May | 0.13 | 0.57 | 0.12 | 0.66 | 4.5 |
| 77 | 16.3 | 9.0 | 1.3 | 0.17 | 5.9 | 7.1 | 7.4 | 12.7 | 16.0 | 17.8 | 346 | 14-Mar | 03-May | 0.08 | 0.35 | 0.10 | 0.40 | 4.7 |
| 78 | 10.3 | 19.5 | 1.4 | 0.39 | 8.0 | 5.8 | 8.1 | 13.2 | 16.9 | 17.3 | 325 | 20-Apr | 02-May | 0.15 | 0.52 | 0.12 | 0.56 | 3.7 |
| 79 | 5.4 | 14.9 | 2.3 | 0.86 | 9.0 | 4.0 | 8.4 | 12.1 | 17.4 | 17.4 | 372 | 11-Apr | 11-May | 0.14 | 0.49 | 0.17 | 0.51 | 4.7 |
| 80 | 10.9 | 19.0 | 3.1 | 0.37 | 10.9 | 1.2 | 8.7 | 13.0 | 16.8 | 17.6 | 405 | 12-Apr | 16-Apr | 0.11 | 0.47 | 0.07 | 0.44 | 4.4 |
| 81 | 10.3 | 10.3 | 2.3 | 0.11 | 8.4 | 0.6 | 9.7 | 14.0 | 16.2 | 18.1 | 443 | 25-Mar | 11-Apr | 0.07 | 0.51 | 0.04 | 0.54 | 3.7 |
| 82 | 13.6 | 10.0 | 2.2 | 0.02 | 7.2 | 0.5 | 8.9 | 13.4 | 18.1 | 19.3 | 571 | 04-Apr | 12-May | 0.10 | 0.53 | 0.11 | 0.58 | 4.1 |
| 83 | 10.5 | 19.7 | 1.2 | 0.02 | 4.3 | 1.2 | 8.6 | 12.2 | 17.6 | 20.2 | 521 | 15-Apr | 25-Apr | 0.15 | 0.48 | 0.12 | 0.49 | 3.8 |
| 84 | 5.3 | 9.6 | 0.5 | 0.03 | 4.1 | 1.8 | 8.7 | 12.2 | 15.7 | 18.2 | 361 | 15-Apr | 22-Apr | 0.15 | 0.37 | 0.13 | 0.38 | 3.4 |
| 85 | 7.4 | 23.5 | 0.8 | 0.06 | 5.6 | 0.7 | 8.9 | 13.5 | 15.6 | 17.7 | 379 | 04-Apr | 09-May | 0.08 | 0.55 | 0.08 | 0.62 | 4.8 |
| 86 | 10.4 | 7.6 | 1.4 | 0.06 | 5.1 | 0.6 | 7.1 | 14.7 | 17.2 | 18.7 | 438 | 23-Apr | 28-Apr | 0.19 | 0.51 | 0.15 | 0.52 | 3.5 |
| 87 | 5.8 | 7.8 | 1.1 | 0.04 | 4.3 | 1.1 | 9.8 | 12.3 | 15.4 | 18.5 | 409 | 08-Apr | 23-Apr | 0.09 | 0.44 | 0.07 | 0.47 | 3.8 |
| 88 | 0.8 | 14.1 | 0.7 | 0.03 | | | 9.5 | 15.1 | 16.1 | 17.9 | 378 | 04-Apr | 19-Apr | 0.12 | 0.42 | 0.08 | 0.43 | 3.7 |
| 89 | 0.7 | 16.6 | | | | | 8.6 | 15.6 | 18.5 | 19.1 | 615 | 27-Mar | 02-May | 0.16 | 0.48 | 0.21 | 0.47 | 5.3 |
| mean | 6.8 | 10.8 | 1.7 | 0.20 | 7.1 | 3.4 | 8.6 | 13.5 | 16.9 | 18.5 | 450 | 07-Apr | 28-Apr | 0.13 | 0.47 | 0.12 | 0.49 | 4.3 |
| c.v. (%) | 64 | 61 | 45 | 106 | 29 | 74 | 9 | 7 | 6 | 5 | 18 | 10 | 7 | 25 | 14 | 35 | 16 | 16 |
| minimum | 0.4 | 1.1 | 0.5 | 0.02 | 4.1 | 0.5 | 7.1 | 12.1 | 15.4 | 17.3 | 325 | 14-Mar | 09-Apr | 0.07 | 0.35 | 0.04 | 0.36 | 3.4 |
| maximum | 16.3 | 23.5 | 3.1 | 0.86 | 10.9 | 8.4 | 10.2 | 15.6 | 18.8 | 20.2 | 615 | 23-Apr | 12-May | 0.19 | 0.59 | 0.21 | 0.66 | 6.0 |

1) no.(10 min trawling)⁻¹2) kg.(10 min trawling)⁻¹3) kg.ha⁻¹4) °C.d⁻¹5) m.s⁻¹

RESULTS

Variations in and correlations among abiotic and biotic factors

The variations in the biotic and abiotic factors over the period 1966-1989 are listed in Table 1. In November age 0 perch were significantly more abundant than age 0 pikeperch, and the YCSV was higher (Table 2). Densities of age 0 perch at the sampling sites were significantly higher in November than in August. For pikeperch, densities were not significantly different between August and November. Perch and pikeperch spawn in the shallow littoral zone (Willemsen 1974). During the first growing season age 0 perch migrate offshore towards the deeper parts of the lake, where most sampling stations are situated. Consequently, mortality estimates for perch over the period August to November are mostly negative. Mortality estimates should therefore be compared relative to other years, and not interpreted as an exact quantification

of the decrease in numbers. Also age 0 pikeperch migrate offshore during the first growing season, but they are caught earlier in the deeper regions of the lake (unpublished data). The mean YCS was for both species similar in the northern and southern part (Table 2). YCS of perch in the two areas were significantly correlated both in August and in November, while for pikeperch they were only significantly correlated in November (Table 3). YCS of perch was significantly correlated with that of pikeperch in the northern part in August as well as in November, and in the southern part only in August.

Table 2. Paired t-tests of recruitment indices ($\log_e(X+1)$). n = number of observations; t_s = Student's t-value; ** $p < 0.01$; *** $p < 0.001$.

| Comparison | | | period | lake part | n | t_s |
|------------------------|-------|---------------------------|--------|-----------|----|----------|
| R_{perch} | Nov | vs $R_{\text{pikeperch}}$ | Nov | north | 20 | 5.48*** |
| R_{perch} | Nov | vs $R_{\text{pikeperch}}$ | Nov | south | 20 | 4.14*** |
| R_{perch} | Aug | vs R_{perch} | Nov | north | 20 | -3.60** |
| R_{perch} | Aug | vs R_{perch} | Nov | south | 20 | -4.68*** |
| $R_{\text{pikeperch}}$ | Aug | vs $R_{\text{pikeperch}}$ | Nov | north | 20 | 0.04 |
| $R_{\text{pikeperch}}$ | Aug | vs $R_{\text{pikeperch}}$ | Nov | south | 20 | -0.81 |
| R_{perch} | north | vs R_{perch} | south | August | 20 | -1.03 |
| R_{perch} | north | vs R_{perch} | south | November | 24 | -0.17 |
| $R_{\text{pikeperch}}$ | north | vs $R_{\text{pikeperch}}$ | south | August | 20 | -1.35 |
| $R_{\text{pikeperch}}$ | north | vs $R_{\text{pikeperch}}$ | south | November | 24 | -0.75 |

Table 3. Coefficient of correlation among recruitment indices ($\log_e(X+1)$). The correlations were done using the longest common time period for each combination. * $p < 0.05$; ** $p < 0.01$.

| | perch | | | | pikeperch | | | |
|---------------------|--------|--------|-------|--------|-----------|--------|-------|--|
| | Aug | north | south | south | Aug | north | south | |
| perch north Nov | 0.77** | | | | | | | |
| perch south Aug | 0.62** | | | | | | | |
| perch south Nov | | 0.71** | | 0.84** | | | | |
| pikeperch north Aug | 0.70** | | | | | | | |
| pikeperch north Nov | | 0.60** | | | 0.50* | | | |
| pikeperch south Aug | | | 0.52* | | 0.36 | | | |
| pikeperch south Nov | | | | 0.36 | | 0.61** | 0.42 | |

Accumulated landings by year-class were correlated significantly with their abundance as age 0 in November surveys for both species (Fig. 4). However, the variation in the landings of perch was much less than the variation in age 0 abundance, whereas they were similar for pikeperch. The landings of pikeperch [77] and [83] lagged behind the expectations based on their age 0 abundance. For [77] this might be due to its small mean size of 11.9 cm, resulting in high first winter mortality, but for [83] no plausible explanation can be given. The abundance index of pikeperch explained less variation in the commercial landings than that of perch.

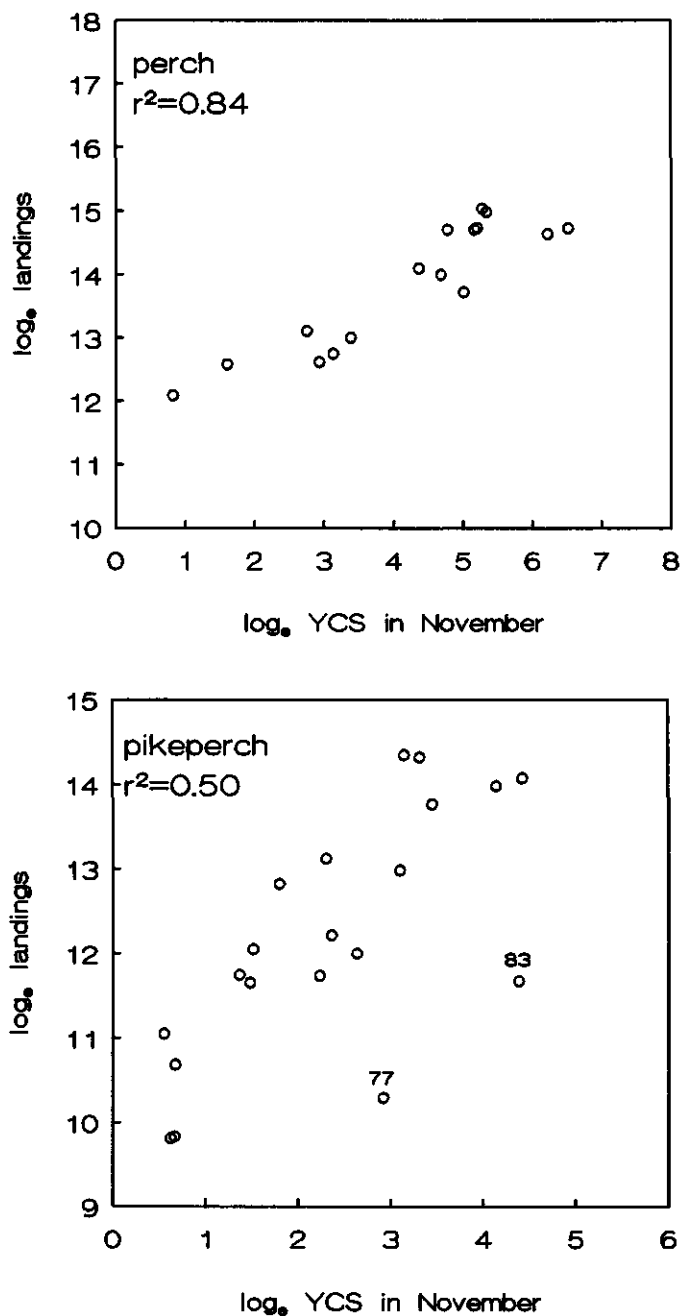


Fig. 4. Log₁₀ accumulated landings of perch (a) and pikeperch (b) in numbers per year-class in the fishery versus their log₁₀ YCS in survey trawl catches in November. YCS = age 0 abundance in survey trawl catches (no.(10 min trawling)⁻¹). Data on age 0 abundance from the northern and southern part were averaged. Data on accumulated landings are given in Appendices 1 and 2.

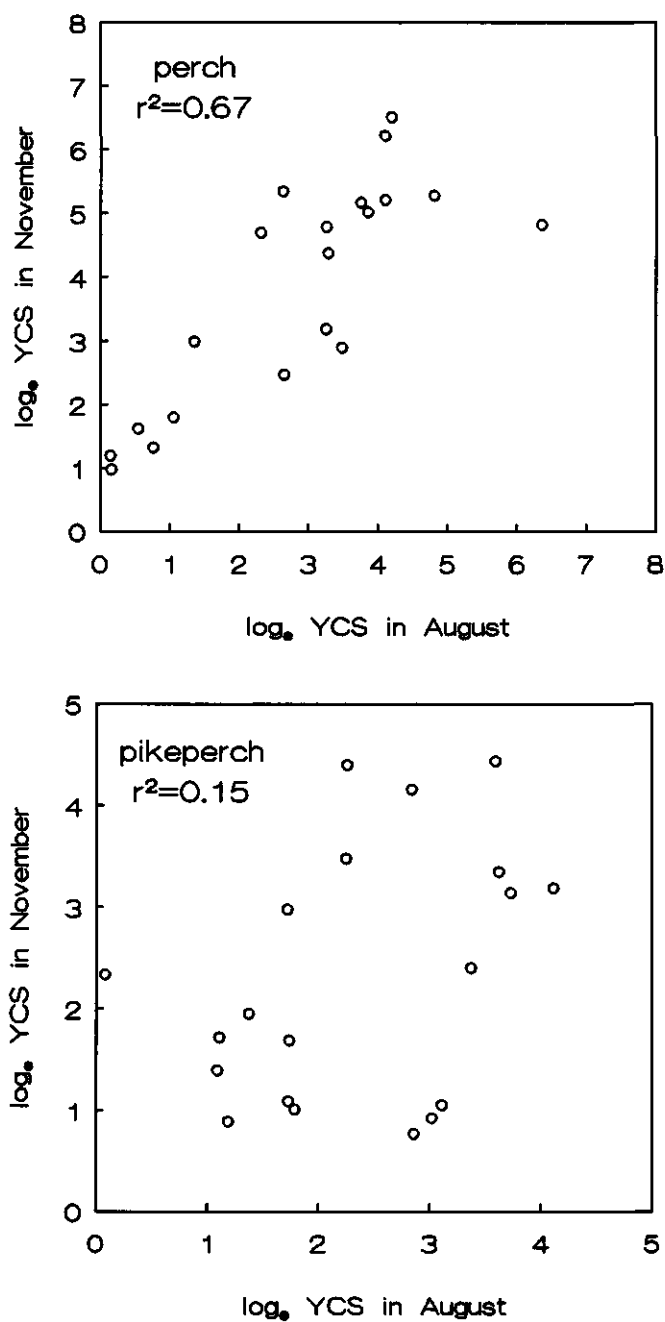


Fig. 5. The log₁₀ YCS estimates of perch (a) and pikeperch (b) in November versus the estimate in August in the period 1966-1973, 1975-1983 and 1987-1989. YCS = age 0 abundance in survey trawl catches (no.(10 min trawling)⁻¹). Data from the northern and southern part were averaged.

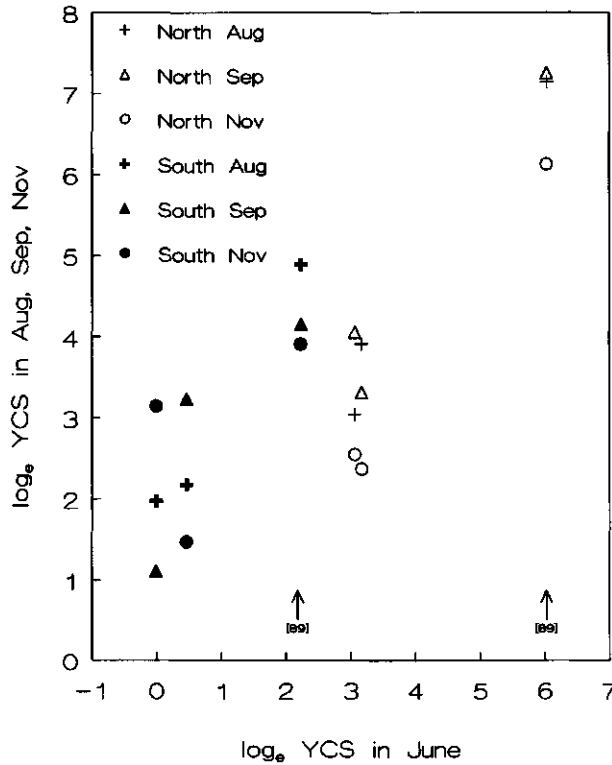


Fig. 6. YCS estimates in August, September and November 1987-1989 versus estimates in June. Estimates are geometric means (adding 1) based on 15 (eight from this study and seven which were for the most part situated in the southeast corner) sampling sites in the northern and seven (five from this study and two additional sites) sampling sites in the southern part (Buijse and Van Densen (000). YCS = age 0 abundance in survey trawl catches (no.(10 min trawling)⁻¹).

YCS of perch appears to be determined already in August, since a highly significant correlation was found with abundance indices in November (Fig. 5), and also with the accumulated landings of the respective year-classes [69]-[73] and [75]-[83] ($r^2=0.65$, $p<0.01$). There is evidence that YCS of perch is already determined in June. Surveys in June showed that already at that time [89] was much stronger than its two predecessors (Fig. 6). YCS of pikeperch in August was not significantly correlated with that in November (Fig. 5). However, correlations between YCS of age 0 pikeperch in August and the accumulated landings of the year-classes [67]-[73] and [75]-[83] ($r^2=0.28$, $p<0.05$) were significant, suggesting that YCS of pikeperch might be determined in August. For pikeperch surveys in June did not indicate that YCS was already determined at that time.

Table 4. Coefficients of correlation among independent variables that were used in the same model. The correlations were done using the longest common time period for each combination. See Table 1 for explanation of the abbreviations.

* $p < 0.05$; ** $p < 0.01$.

| | | | smelt biom Aug s | smelt biom Aug n | smelt biom Aug 1) | smelt biom Nov s | smelt biom Nov n | smelt biom Nov 1) | smelt length Nov s | smelt length Nov n | smelt length Nov 1) | perch psb s | perch psb n | perch psb 1) | log, perch ssb | log, pikep ssb |
|-------------|----------|--------|-----------------------------|---------------------------|----------------------------|---------------------------|---------------------------|----------------------------|-----------------------------|-----------------------------|------------------------------|-------------------|-------------------|--------------------|----------------------|----------------------|
| year | | | | | | | | | | | | | | | | |
| lt | biom | Aug s | 0.03 | | | | | | | | | | | | | |
| lt | biom | Aug n | 0.24 | | | | | | | | | | | | | |
| lt | biom | Aug 1) | 0.18 | | | | | | | | | | | | | |
| lt | biom | Nov s | -0.14 | -0.02 | | | | | | | | | | | | |
| lt | biom | Nov n | 0.15 | | 0.43 | | | | | | | | | | | |
| lt | biom | Nov 1) | 0.03 | | | 0.38 | | | | | | | | | | |
| lt | length | Nov s | 0.02 | 0.31 | | | 0.22 | | | | | | | | | |
| lt | length | Nov n | 0.33 | | 0.16 | | | 0.27 | | | | | | | | |
| lt | length | Nov 1) | 0.25 | | | 0.47* | | 0.27 | | | | | | | | |
| rch | psb | s | 0.26 | 0.32 | | | 0.03 | | -0.14 | | | | | | | |
| rch | psb | n | 0.58** | | 0.17 | | | 0.32 | | 0.17 | | | | | | |
| rch | psb | 1) | 0.55** | | | 0.39 | | | | | 0.26 | | | | | |
| perch | ssb | | -0.59** | | | 0.04 | | | | | 0.38 | | | | | |
| perch | ssb | | -0.70** | | | 0.06 | | | | | 0.30 | | | | | |
| perch | ssb | | | | | | | | | | 0.35 | | | | | |
| piscivorous | stock 2) | | -0.90** | | | -0.05 | | | | | | | | | 0.61* | |
| perch | psb | | -0.77** | | | -0.37 | | | -0.25 | | | | | | | 0.57* |
| | Apr | | 0.23 | -0.14 | 0.26 | 0.11 | 0.26 | 0.34 | 0.34 | 0.04 | 0.19 | 0.16 | -0.10 | 0.05 | -0.01 | 0.00 |
| | May | | 0.01 | -0.18 | -0.11 | -0.17 | -0.45* | -0.33 | -0.43* | 0.10 | 0.05 | 0.08 | -0.37 | -0.21 | -0.34 | 0.00 |
| | Jun | | -0.20 | 0.08 | -0.15 | -0.06 | -0.10 | 0.05 | -0.01 | 0.13 | 0.31 | 0.29 | -0.04 | -0.14 | -0.12 | 0.52* |
| | JulAug | | -0.05 | -0.25 | 0.06 | -0.08 | 0.00 | 0.05 | 0.04 | 0.08 | 0.08 | 0.10 | 0.04 | -0.08 | -0.03 | 0.14 |
| | dd14 | | -0.07 | -0.21 | 0.12 | -0.02 | -0.02 | 0.01 | -0.01 | 0.29 | 0.21 | 0.30 | -0.08 | -0.09 | -0.11 | 0.40 |
| | dano8 | | -0.00 | 0.00 | -0.37 | -0.26 | 0.08 | -0.10 | -0.03 | | | 0.30 | -0.13 | 0.07 | -0.01 | -0.02 |
| | dano11 | | -0.13 | 0.25 | -0.28 | -0.07 | -0.28 | -0.30 | -0.33 | -0.30 | -0.08 | -0.21 | | | | 0.18 |
| | roi8 | | -0.01 | 0.03 | -0.38 | -0.25 | -0.06 | 0.11 | 0.04 | | | | -0.26 | 0.03 | -0.10 | -0.01 |
| | roi11 | | -0.08 | 0.16 | -0.23 | -0.08 | -0.15 | 0.12 | 0.01 | 0.26 | 0.17 | 0.25 | | | | 0.30 |
| | sd8 | | -0.01 | -0.01 | -0.14 | -0.11 | 0.01 | -0.09 | -0.06 | | | | -0.02 | -0.07 | -0.06 | 0.35 |
| | sd11 | | 0.00 | 0.08 | -0.11 | -0.04 | -0.05 | -0.11 | -0.09 | -0.27 | 0.35 | 0.12 | | | | 0.06 |
| | wind8 | | -0.39 | 0.22 | 0.22 | 0.28 | 0.10 | 0.22 | 0.19 | | | | -0.03 | 0.25 | 0.22 | 0.27 |
| | wind11 | | -0.64** | -0.10 | -0.07 | -0.10 | 0.45 | 0.32 | 0.42 | -0.14 | -0.08 | -0.13 | | | | 0.72** |
| | | | pisc. stock psb 2) | perch psb | | | | | | | | | | | | |
| | | | | | Apr | May | Jun | JulAug | dd14 | dano8 | dano11 | roi8 | roi11 | sd8 | sd11 | |
| | Apr | | 0.21 | -0.29 | | | | | | | | | | | | |
| | May | | 0.05 | 0.03 | -0.11 | | | | | | | | | | | |
| | Jun | | 0.21 | -0.10 | -0.33 | 0.35 | | | | | | | | | | |
| | JulAug | | 0.15 | 0.06 | -0.10 | 0.01 | 0.23 | | | | | | | | | |
| | dd14 | | 0.02 | -0.08 | -0.12 | 0.31 | 0.61** | 0.83** | | | | | | | | |
| | dano8 | | 0.17 | -0.32 | -0.02 | 0.17 | 0.17 | 0.05 | | | | | | | | |
| | dano11 | | | 0.27 | -0.54** | 0.03 | 0.32 | 0.23 | 0.28 | | | | | | | |
| | roi8 | | 0.11 | | -0.52** | 0.13 | 0.57** | 0.17 | 0.26 | 0.61** | | | | | | |
| | roi11 | | | 0.09 | -0.56** | 0.14 | 0.70** | 0.17 | 0.40 | | 0.40 | | | | | |
| | sd8 | | 0.22 | | -0.09 | 0.37 | 0.53** | -0.07 | 0.18 | 0.33 | | 0.23 | | | | |
| | sd11 | | | -0.32 | -0.08 | 0.29 | 0.40 | 0.02 | 0.18 | | 0.42* | | 0.06 | | | |
| | wind8 | | 0.51 | | -0.23 | 0.06 | 0.37 | 0.14 | 0.38 | -0.48 | | -0.05 | | 0.06 | -0.19 | |
| | wind11 | | | 0.53* | -0.02 | -0.33 | -0.26 | -0.21 | -0.30 | | -0.29 | | -0.13 | | -0.27 | |

1) Smelt biomass in August and November, smelt length and stock biomass of piscivorous based on trawl surveys were calculated by averaging the value from the northern and southern part.

2) Stock biomass of piscivores was estimated by adding up stock biomass of piscivorous perch and pikeperch based on cohort analysis.

Smelt biomass, which consisted almost exclusively of age 0 and age 1 fish, varied less than YCS of both percids. Length of age 0 smelt was significantly smaller (mean difference = 0.6 cm) in the southern part than in the northern part (paired t-test: $t_s = 4.81$, $p < 0.001$, $n = 23$). Smelt was larger in November

when biomass of smelt in August was higher (Table 4). The high biomass might have been the result of a large mean length in August, but unfortunately lengths have not been measured in August. Smelt biomass in August and November were not significantly correlated, which might indicate that November data were not representative for biomass during summer. There is evidence, however, that November data are representative for the availability of smelt during summer. Data which were collected from 1987 to 1989 showed significant correlations with surveys earlier that year (Table 5): densities of age 0 smelt in November correlated significantly with those collected in June and in September; length of age 0 smelt in November correlated with those in August and September.

Table 5. Coefficients of correlation between total lengths and between abundancies of age 0 smelt in four sampling periods from 1987-1989. $n=6$; * $p<0.05$; ** $p<0.01$. Data from Buijse and Van Densen (000).

| | total length (cm) | | | log _e abundance (no. (1000 m trawling) ⁻¹) | | |
|-----|-------------------|--------|--------|---|-------|--------|
| | Jun | Aug | Sep | Jun | Aug | Sep |
| Aug | -0.12 | | | 0.88* | | |
| Sep | -0.23 | 0.99** | | 0.97** | 0.91* | |
| Nov | -0.24 | 0.99** | 0.97** | 0.90* | 0.76 | 0.93** |

Both stocks of perch and pikeperch are exploited heavily in Lake IJssel. The landings per age-group and year-class and the estimated instantaneous fishing mortality rates are listed in Appendix 1 and 2 for perch and pikeperch respectively. The mean exploitation pattern for perch shows that exploitation actually starts at age 3 (Fig. 7). Exploitation of age 4 to 6 fish was not significantly different. Pikeperch is mainly exploited at age 2 and 3, while exploitation of age 4 fish was significantly lower. It is clear that pikeperch is heavily exploited prior to maturation of the females at age 3 or 4. Yearly fishing mortalities varied largely from year-to-year for perch and pikeperch (Appendix 1 and 2). This variation is partly due to variable age at recruitment to the fishery: consecutive warm summers result in an earlier recruitment. Some variation might be caused by sampling procedures, because market sampling was limited in some years.

Stock biomass of piscivorous perch and pikeperch based on cohort analysis combined, varied from 15.8 kg.ha⁻¹ (1975) to 5.4 kg.ha⁻¹ (1987). Stock biomass of piscivorous perch was on average circa 2 times higher than that of pikeperch, while spawning stock biomass was on average 8-9 times higher. The spawning stock biomass of pikeperch severely declined at the beginning of the eighties, and was always less than 0.07 kg.ha⁻¹ thereafter. The mean ratio between the spawning and the piscivorous stock biomass was 0.24 and 0.09 for perch and pikeperch respectively. Not surprisingly, piscivorous and spawning stock biomass (based on cohort analysis) were positively correlated (Table 4), but

since information on age at maturity and onset of piscivory was available we preferred to differentiate between producer and consumer stock biomass. Year of sampling was positively correlated with stock biomass of piscivorous perch (based on trawl surveys), and negatively with stock biomass of spawning and piscivorous perch and pikeperch (based on cohort analysis).

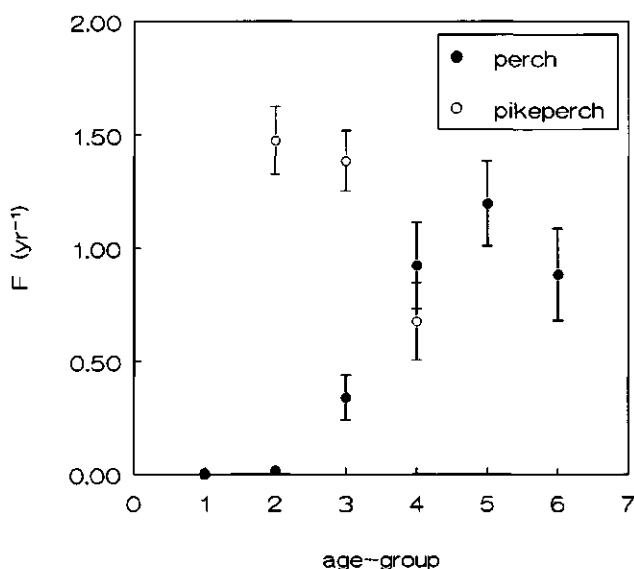


Fig. 7. Estimated mean exploitation pattern of year-class [69] to [81] of perch, and of year-class [67] to [83] of pikeperch. F = instantaneous fishing mortality rate. Errors bars depict the SE. Data are based on Appendices 1 and 2 for perch and pikeperch respectively.

The stock biomass of piscivorous perch based on trawl surveys for the two lake parts combined varied more than those based on the cohort analyses and the correlation between the two was not significant ($r=0.30$, $n=15$, $p>0.25$). The estimate based on the cohort analysis is thought to be the more reliable, because commercial landings sampled a much greater part of a year-class than trawl surveys did, and was therefore used in the analysis which combined for both lake parts.

Mean monthly water temperatures varied by 3.1, 3.5, 3.4°C in April, May and June, and mean bimonthly water temperature varied 2.9°C in July - August (Table 1). Based on the Julien date when water temperature exceeded the required value for reproduction, spawning of perch is estimated to have started in some years as early as in the second half of March, but to have been postponed until the end of April in other years. Likewise, spawning of

pikeperch did not start before mid April, and had been postponed until mid May. Average warming rates from Julian date when water temperature exceeded 8°C and 11°C until June 21 were 0.13 and 0.12 °C.d⁻¹ respectively. Warming rate was high when temperatures were low in April or high in June, which is the result of the period over which the warming rate was calculated (Table 4). Warming rate was faster when the date when temperature first raised above 8°C (DANO8) was late. When temperatures in April were low, the date upon which the temperature exceeded 11°C (DANO11) was late. The sum of degree days over 14°C correlated positively with mean temperatures in June and July - August, which is obvious, because mean temperature never was below 14°C in these months.

Other significant correlations among independent variables (May temperature - smelt biomass; wind - year; June temperatures - spawning stock biomass of perch and day-to-day variation in temperature (SD8); DANO11 - SD11) were considered spurious.

Recruitment models

For perch 5 out of 7 models tested were significant and 36% to 71% of variations in YCS could be explained (Table 6). Early warming during spring had a negative effect on year-class formation as reflected by the negative correlation with water temperature in April, and the positive correlation with DANO8. A rapid warming rate thereafter had a positive influence on year-class formation. A warm summer indexed by water temperatures in July and August, and the sum of degree days above 14°C, had a positive effect on YCS. YCS in the northern part in August was significantly positively correlated with year of sampling. Mortality between August and November was surprisingly negatively correlated with stock biomass of piscivores.

For pikeperch 6 out of 8 models tested were significant and 38% to 86% of variations in YCS could be explained (Table 7). Only abiotic factors significantly explained part of the variation in YCS. Low temperatures in April, and high temperatures from June to August favoured year-class formation. YCS in the southern part was significantly negatively correlated with year of sampling.

Table 6.

Fraction explained variation and parameter estimates for linear models of log_e abundance (adding 1) and mortality of age 0 perch in the northern and southern part of Lake IJssel in August and November on various biotic and abiotic factors. i=included in the analysis but not significant in explaining recruitment variations. The variables "May", "Jun" and "sd8" were used in model 1 to 6, but these variables never reduced a significant part of the variation (See Table 1 for explanation of the abbreviations). ns=none of the variables significantly reduced the variation; * p<0.05; ** p<0.01; *** p<0.001.

| | period ¹⁾ | R ² | smelt | | perch ³⁾ | | log _e | | perch + ⁴⁾ | | dd14 | dano8 | roi8 | wind8 ²⁾ | year |
|--|----------------------|----------------|-------|------|---------------------|-----|------------------|--------|-----------------------|---------|--------|--------|------|---------------------|------|
| | | | biom | biom | psb | psb | ssb | psb | psb | psb | | | | | |
| 1. log _e age 0 abundance in Lake IJssel in August | 73, 75-83, 87 | ns | i | i | i | i | i | i | i | i | i | i | i | i | i |
| 2. log _e age 0 abundance in Lake IJssel in November | 73-87 | 0.36 | i | i | i | i | i | i | i | i | i | 0.080* | i | i | i |
| 3. log _e age 0 abundance in the southern part in August | 66-73, 75-83, 87-89 | ns | i | i | i | i | i | i | i | i | i | i | i | i | i |
| 4. log _e age 0 abundance in the southern part in November | 66-89 | 0.50 | i | i | 0.29** | i | i | i | i | i | i | i | 32** | i | i |
| 5. log _e age 0 abundance in the northern part in August | 66-73, 75-83, 87-89 | 0.66 | i | i | i | i | i | 0.72* | i | i | i | i | 23* | 0.15*** | i |
| 6. log _e age 0 abundance in the northern part in November | 66-89 | 0.71 | i | i | 0.13*** | i | i | -0.67* | i | 0.010** | 0.062* | i | i | i | i |
| 7. log _e mortality of age 0 from August to November | 73, 75-83, 87 | 0.37 | i | i | i | i | i | -0.17* | i | i | i | i | i | i | i |

1) The years excluded from the analyses vary due to missing data (Table 1)

2) Wind velocity, for which data were only available from 1973 onwards, did not have a significant influence. Wind velocity was therefore excluded from further analyses so that years prior to 1973 could be included.

3) Stock biomass of piscivorous perch as estimated by trawl surveys in November

4) Sum of stock biomass of piscivorous perch and pikeperch as estimated by cohort analysis of the commercial landings.

Table 7.

Fraction explained variation and parameters estimates for linear models of log_e abundance (adding 1) and mortality of age 0 pikeperch in the northern and southern part of Lake Ussel in August and November on various biotic and abiotic factors. i=included in the analysis but not significant in explaining recruitment variations. The variable "smelt length Nov" was used in all models, and the variables "May", "dano11", "roi11" and "sd11" were used in model 1 to 7, but these variables never reduced a significant part of the variation (See Table 1 for explanation of the abbreviations). ns=none of the variables significantly reduced the variation; * p<0.05; ** p<0.01; *** p<0.001.

| | period ¹⁾ | R ² | smelt biom Aug | smelt biom Nov | log _e pikep ssb | pikep psb | Apr | Jun | JulAug | ddl4 | wind11 ²⁾ | year |
|----|---|----------------|----------------------|----------------------|----------------------------------|--------------|--------|-------|---------|------|----------------------|----------|
| 1. | log _e age 0 abundance in Lake Ussel in August | 0.39 | i | i | i | i | i | 0.63* | i | i | i | i |
| 2. | log _e age 0 abundance in Lake Ussel in November | 0.70 | i | i | i | i | i | i | 1.04*** | i | i | i |
| 3. | log _e age 0 abundance in the southern part in August | 0.86 | i | i | i | i | i | i | i | i | -1.35** | -0.31*** |
| 4. | log _e age 0 abundance in the southern part in August | 0.41 | i | i | i | i | -2.00* | i | i | i | i | i |
| 5. | log _e age 0 abundance in the southern part in November | 0.38 | i | i | i | i | i | i | 0.60* | i | i | -0.08* |
| 6. | log _e age 0 abundance in the northern part in August | ns | i | i | i | i | i | i | i | i | i | i |
| 7. | log _e age 0 abundance in the northern part in November | 0.58 | i | i | i | i | -0.57* | i | 1.06*** | i | i | i |
| 8. | log _e mortality of age 0 from August to November | ns | i | i | i | i | i | i | i | i | i | i |

1) The years excluded from the analyses vary due to missing data (Table 1)

2) Wind velocity, for which data were only available from 1973 onwards, did not have a significant influence for the other models. Wind velocity was therefore excluded from further analyses so that years prior to 1973 could be included.

Stock-recruitment relationships

No direct relation between spawning stock and recruitment (SR) was observed (Fig. 8). For perch, the variation in recruits is much higher than the variation in spawners. Strong year-classes of pikeperch were produced even when the spawning stock biomass was very low ($0.02 \text{ kg} \cdot \text{ha}^{-1}$). The relation between spawning stock biomass and recruitment might be obscured by abiotic and biotic factors influencing survival of age 0 fish, but in the recruitment models, which evaluated the combined effect of these factors, spawning stock biomass was never included as an explanatory variable.

Comparison of YCS of percids in various water bodies.

YCSV of perch in Lake IJssel fell outside the range of YCSV observed for *Perca* spp. in other water bodies, while YCSV of pikeperch fell within the range observed for *Stizostedion* spp.. Variations in YCS of percids in other water bodies were compared with those of perch and pikeperch in Lake IJssel (Fig. 9 and 10). Methods used to index YCS include trawling and seining for age 0 fish (e.g. Oneida Lake, Lake Erie, Lake IJssel), trap net fishing during the spawning period (Windermere), VPA (Lake Constance), mark-recapture (Escanaba Lake), contribution to the commercial fishery (Red Lakes), adding catches of a year-class in successive years (Lake Hjälmaren and Mälaren). Not all of these methods will yield the same estimate in a particular situation. Thus, the possibilities for comparison of the amplitude of fluctuation in YCS between water bodies is limited (Koonce et al. 1977). Still, a general insight in the magnitude of YCSV of percids might be expected. YCSV was characterised by the \log_e SD of YCS (adding 1) (Pitcher and Hart 1982, p. 212). For *Perca* spp. YCSV varied from 1.00 in Red Lakes and Oneida Lake to 1.73 in western Lake Erie. In Lake IJssel variation for perch was 1.83 and 1.87 in the northern and southern part respectively. For *Stizostedion* spp. YCSV varied from 0.73 in Lake Lewis and Clark to 1.57 in Lake Francis Case. In Lake IJssel variation for pikeperch was 1.35 and 1.20 in the northern and southern part respectively. YCSV appeared to be generally higher for *Perca* spp. than for *Stizostedion* spp..

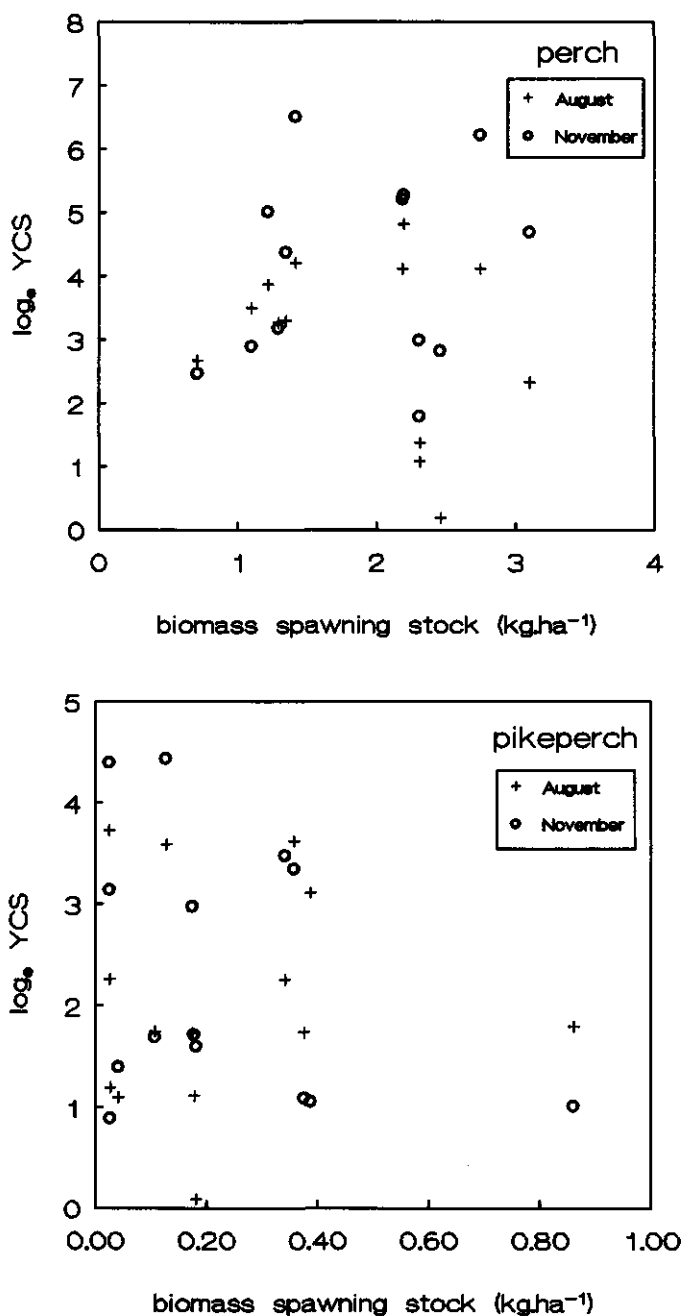


Fig. 8. The log₁₀ YCS estimates of age 0 perch (a) and pikeperch (b) in August and November in relation to spawning stock size. YCS = age 0 abundance in survey trawl catches (no./10 min trawling⁻¹).

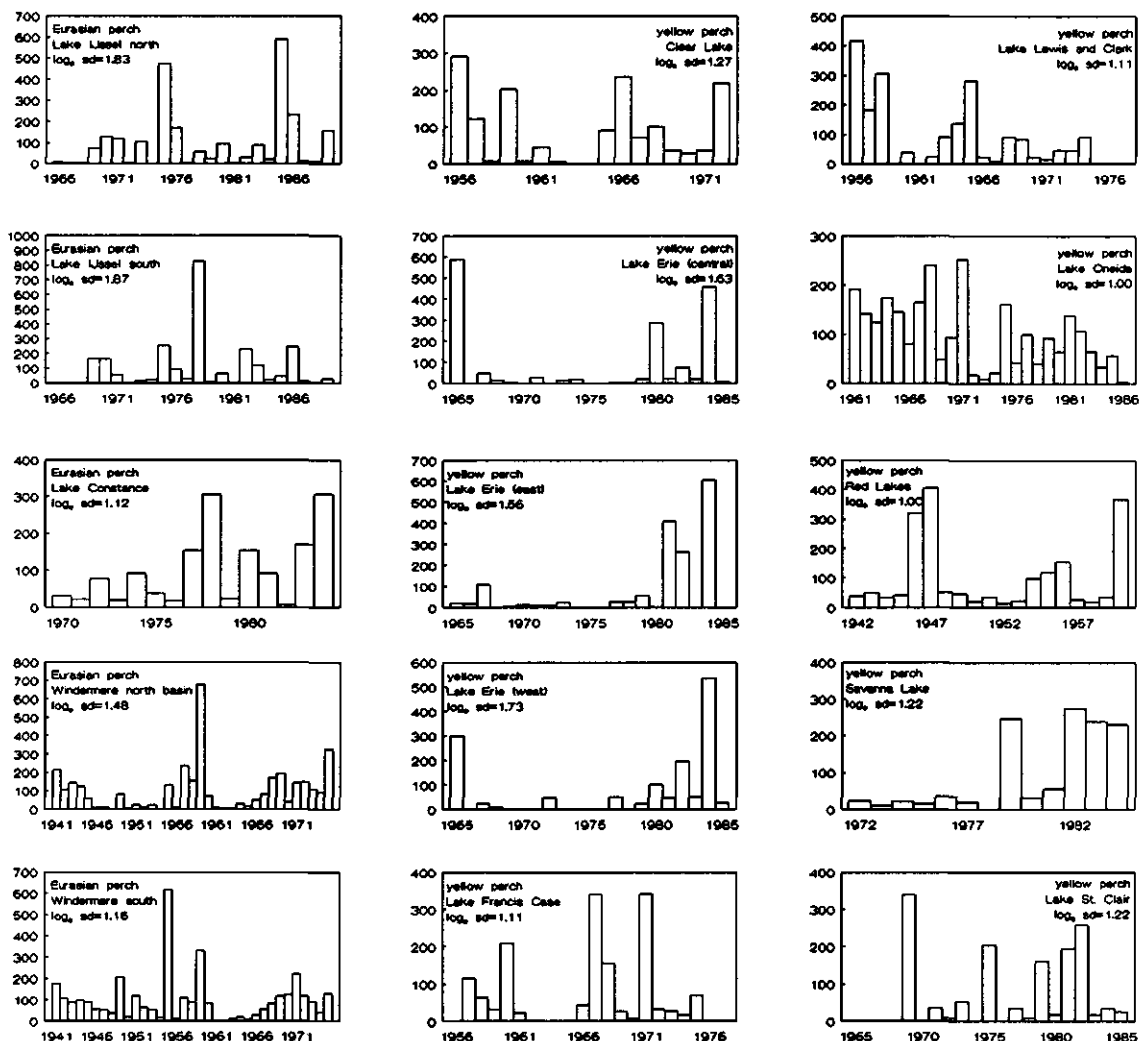


Fig. 9. Year-class strength (YCS) of perch and yellow perch in 13 ecosystems, standardised for the mean YCS: $YCS = 100 * YCS / (\text{mean } YCS)$. \log_{10} SD = standard deviation of the logarithm (adding 1) of the YCS. Source: Lake Constance (Hartmann and Blank 1989); Windermere (Craig et al. 1979); Clear lake (Carlander and Payne 1977); Lake Erie and St. Clair (Henderson and Nepszy 1988); Lake Francis Case and Lake Lewis and Clark (Nelson and Walburg 1977); Lake Ussel (this study); Oneida Lake (Mills and Forney 1988); Red Lakes (Smith Jr. 1977); Lake Savanna (Ritchie and Colby 1988).

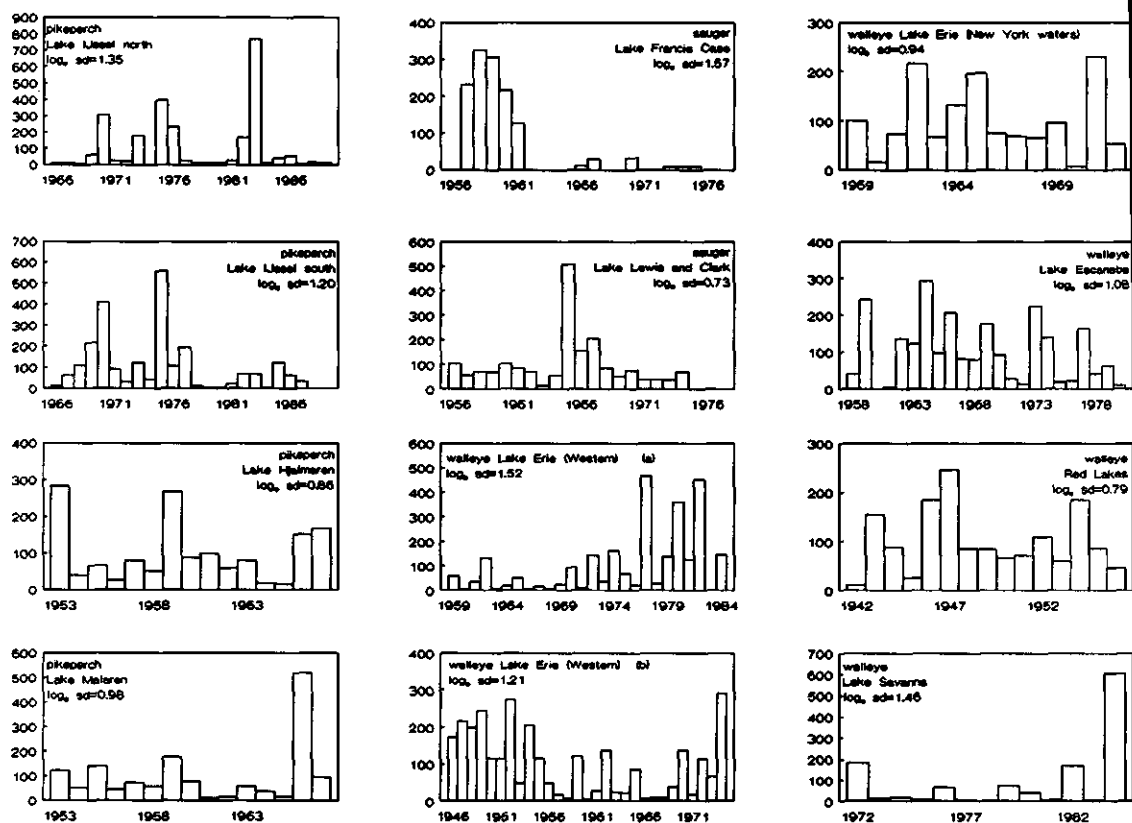


Fig. 10. Year-class strength (YCS) of pikeperch, walleye and sauger in 10 ecosystems, standardised for the mean YCS: $YCS = 100 \cdot YCS_i / (\text{mean } YCS)$. $\log_e SD$ = standard deviation of the logarithm (adding 1) of the YCS. Source: Lake Hjälmaren and Mälaren (Svärdson and Molin 1973); Lake Francis Case and Lake Lewis and Clark (Nelson and Walburg 1977); Lake Erie (a. western age 0 fish: Hatch et al. 1987, b. western age 1 fish: Shuter and Koonce 1977, New York waters: Wolfert 1981); Escanaba Lake (Serns 1982); Lake IJssel (this study); Red Lakes (Smith Jr. 1977); Lake Savanna (Ritchie and Colby 1988).

DISCUSSION

YCS of perch and pikeperch in Lake IJssel will probably always be highly variable, because it is a common phenomenon for percids (Koonce et al. 1977). Mean YCSV of *Perca* spp. ($\log_e SD = 1.35$) and *Stizostedion* spp. (1.14) stocks are higher than the mean YCSV of a number of stocks of 11 marine fish species except haddock, *Melanogrammus aeglefinus* (1.26) (Hennemuth et al. 1980). Mean YCSV were 0.40 for cod, *Gadus morhua*, 0.47 for saithe, *Pollachius*

virens, and 0.62 for herring, *Clupea harengus* (0.62) (Pitcher and Hart 1982, p. 212).

The use of many variables in trying to explain YCSV has the inherent danger that spurious correlations might emerge. To avoid this problem as much as possible, the factors studied were based on hypotheses derived from studies on other percid populations (Oneida Lake, Windermere) and on established interactions among fish species in Lake IJssel.

A few other studies applied regression analysis of long-term series to explain variation in YCS of percids. Variations in densities of age 0 walleye in autumn were investigated in relation to water temperature, wind, and adult walleye density in Escanaba Lake by Serns (1982), who observed that the coefficient of variation of May temperatures were negatively correlated with YCS. Henderson and Nepszy (1988) used stock size and water temperature to explain age 1 abundance of yellow perch in Lake Erie and Lake St. Clair in May and June. Age 1 abundance in western lake Erie was positively correlated with warming rate from April to June and stock size. Recruitment of walleye in Lake Erie was correlated positively with breeding stock size and the rate of water temperature increase in spring (Shuter and Koonce 1977). In Windermere, adult biomass of perch and water temperature in the year of hatching and age 2 pike (*Esox lucius*) cohort strength were used to explain the abundance of age 2 perch in the northern and southern basin (LeCren 1987; Mills and Hurley 1990). YCS was positively related with the sum of degree days over 14°C, while a dome-shaped relation in the north and a negative relation in the south between YCS and adult biomass was observed. Cohort strength of pike did not influence year-class formation of perch significantly.

Temperature and wind versus recruitment

Results showed that temperature has a significant influence on year-class formation of both species. In Lake IJssel, physiological optimum temperatures of 27.3 °C for pikeperch and 25.4 °C for perch (Hokanson 1977) are not reached. Both species will thus profit from high temperatures, given a sufficient supply of food.

Effects of temperature during spring might offer the most plausible causal relationship, because YCS of perch appeared to be determined already by the end of June. Postponed spawning due to late warming and thereafter a rapid development of eggs and larvae due to a high warming rate of Lake IJssel could favour year-class formation. Development of perch eggs is faster at higher temperatures (Guma'a 1978; Kokurewicz 1969; Treasurer 1983). If the experimental data on the influence of temperature on egg development by Kokurewicz (1969) and Guma'a (1978) are expressed as degree days above 6°C,

a constant sum of degree days of 93, over a wide range of incubation temperatures (9-22°C), is needed for hatching. Willemsen (1977) mentioned that perch spawn at 8-12°C in lake IJssel. If all perch spawned at 8°C, the time period to hatch (93 degree days over 6°C) could have varied from 15 to 52 days, while at 12°C it would still have varied between 9 and 26 days. So hatching in Lake IJssel could seriously have been delayed in years when warming rate was slow. In Lake Michigan, early hatched bloater (*Coregonus hoyi*) experienced a higher mortality (Crowder et al. 1987). Rapid and intensive warming up in 1966 coincided with a strong year-class of pikeperch in Lake Mälaren (Svärdson and Molin 1981). High May temperatures favoured year-class formation of walleye in Escanaba Lake (Serns 1982). Since eggs and larvae have little or no mobility, they cannot respond to changes in the local physical environment. Highest mortality of perch in Loch Kinord occurred during the eleuthero-embryonic phase possibly through mechanical damage of newly-hatched embryos (Treasurer 1983). Since mortality declines with size (Peterson and Wroblewski 1984), size-dependent survival during the larval and pre-recruit phase from April to June (Anderson 1988; Miller et al. 1988), is probably important for year-class formation of perch. Based on literature data on effects of temperature on life history stages of marine fish, Pepin (1991) concluded that higher temperatures resulted in faster growth and higher mortality, by which the net effect on survival is likely to be minor.

Wind velocity contributed to the explanation of the YCS of age 0 pikeperch in the southern part in August only. Since the correlation between wind velocity and year of sampling might have been a spurious one, the negative correlation between wind velocity and abundance of age 0 pikeperch might also be spurious. We conclude therefore that wind velocity did not affect recruitment in this case.

Most correlations between abundance in the northern and southern part of age 0 perch and pikeperch were significant, which could indicate that climatic factors indeed play an important rôle in year-class formation. The northern and southern part of Lake IJssel were not fully separated until 1975. Construction of the dyke started as early as 1963, 22% was completed in 1966, 46% in 1968, and 74% in 1972. Based on a tagging programme carried out in 1969-75, Willemsen (1977) concluded that the majority of adult perch and pikeperch do not migrate extensively. 80% of the pikeperch that were captured and released in the northern part were recaptured in the northern part, while in the southern part this was even 93%. For perch, the corresponding percentages were 91% and 87% in the northern and southern part respectively. Extrapolation of these results to age 0 fish is limited. Still, we think that migration of age 0 fish was not extensive between the northern and the southern part, but only between the shallow spawning areas and the deeper regions. If so estimates of YCS for the

northern and southern part can be regarded as separate indices, also prior to 1975.

Predation and alternative fish prey versus recruitment

Piscivorous stock biomass did not influence YCS of the two species in Lake IJssel. Although a positive correlation was observed between YCS of perch and stock biomass of piscivores this was considered not a causal one. The positive correlation might suggest that recruitment critically depends on spawning stock biomass, but since both stock biomass and age 0 abundance show a time trend, it is assumed that the commercial trawl fishery before 1970 had a similar effect on both parameters.

In Lake IJssel the buffering capacity of smelt and the heavy impact of the fishery on perch and pikeperch appeared to have diminished the predatory influence by the parental stock of perch and pikeperch on their offspring. According to the available literature, alternative prey abundance may buffer predation on percids. Smelt appeared to smooth the interaction between walleye and perch in Lake Hjälmaren (Svärdson 1976). In some Swedish lakes strong perch year-classes emerged when there was a good supply of roach, bleak (*Alburnus alburnus*) and smelt, but in the absence of alternative fish prey no strong year-class was formed when a preceding strong year-class was still abundant (Alm 1952). *Hexagenia limbata* effectively reduced walleye cannibalism in Savanna Lake (Ritchie and Colby 1988). YCS of yellow perch, being the major prey of walleye in Oneida Lake, is negatively influenced by walleye densities (Forney 1980; Nielsen 1980), while cannibalism on age 0 walleye is buffered by age 0 yellow perch (Forney 1974, 1976). In Lake Constance a heavy exploitation of the perch stock is permitted to reduce cannibalism, which is not buffered by alternative prey (Staub et al. 1987).

Onset of piscivory was found to be crucial in year-class formation of pikeperch, and is favoured by high temperatures (Buijse and Houthuijzen 1992) and a high availability of fish prey (Van Densen 1985). Pikeperch became piscivorous in the neighbouring Tjeukemeer in June, and the process was triggered by a high availability of age 0 smelt (Van Densen 1985). In Lake IJssel, however, availability of age 0 smelt was not found to influence year-class formation of pikeperch. Indices for (alternative) prey availability during the summer were based on data collected during August and November trawl surveys. These data reflect their availability as fish prey, but moreover they show that smelt was abundant, and as such probably never limiting for the onset of piscivory. We conclude that given the abundant supply of smelt variations in summer temperatures are more important in determining YCSV of age 0 pikeperch.

Shortcomings of the analysis

There is evidence that both the commercial fishery and fish-eating birds have a considerable impact on the fish stocks in Lake IJssel. The fishery in Lake IJssel has changed considerably over the period investigated (Dekker 1991; Van Densen et al. 1990). Commercial trawling for eel was allowed until 1970, whereafter this gear was banned because of the large by-catch of forage fish including juvenile perch and pikeperch. After the ban on trawling, the fishermen started to catch eel with movable fyke nets, which are set in the open water area (Van Densen et al. 1990). The by-catch in this fyke net fishery comprises, among others, juvenile perch and pikeperch. The numbers of fyke nets have increased sharply from $\pm 12,000$ in 1970 to $\pm 47,000$ in 1985 when a ceiling was prescribed for the number of nets (Dekker 1991). By that time, the mortality induced by the fyke fishery on immature percids was once again high (Willemsen 1985). The positive correlation between stock biomass of piscivorous perch based on experimental trawl surveys and year of sampling might have arisen from the low stock of perch prior to 1970 caused by the commercial trawl fishery. When only the period since 1970 is considered a negative correlation between estimates of stock biomass based on cohort analysis and year of sampling was found, which might have been induced by the increased mortality by the fyke net fishery.

Besides a variable impact of the eel fishery the intensity of bird predation has increased over the investigated period, especially through the number of cormorants (*Phalacrocorax carbo*) (Van Eerden and Zijlstra 1985). Preliminary estimates of bird predation on perch amounted $13.6 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in the period 1983 - 1987, of which 54% was eaten by cormorants, while the estimated production of perch was $19.2 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at that time (Buijse et al. 1991). Although the influence of bird predation and eel fishery on year-class formation of both species is obvious, they could unfortunately not be included in the analysis. Time series for birds were not available for the whole period and species composition of the landed (trawl) or discarded (fyke nets) by-catch was not known. So the varying impact of bird predation and the fishery might have obscured relations between year-class formation and in this paper presented abiotic and biotic factors.

Research and management implications

An evaluation which abiotic and biotic factors contribute to the variation in recruitment has implications for the fisheries management of the gill net fishery in Lake IJssel. Based on an evaluation of a 24-year time series, we conclude that temperature appears to have a strong influence on recruitment of pikeperch

and perch, while stock-recruitment relationships were not demonstrated. Since abiotic factors are difficult to manage, further research on environmental factors might yield little useful information for the management of the fishery. So from a manager's point of view, exploitation of perch and pikeperch could thus be maximised in terms of yield-per-recruit, and recruitment to the fishery could be predicted by simply monitoring age 0 abundance in November. We conclude that this would be a simple autecological approach to fisheries management, underutilizing existing knowledge on the Lake IJssel ecosystem.

The present small spawning stock biomass of pikeperch and the large biomass of prey fish in our opinion indicate better prospects for stock enlargement and higher yields than those expected from optimising yield-per-recruit. Spawning stock biomass of pikeperch in Lake IJssel has always been very low ($0.02 - 0.86 \text{ kg.ha}^{-1}$) when compared to e.g. spawning stock biomass of walleye in Oneida Lake ($8.3 - 12.4 \text{ kg.ha}^{-1}$ (Forney 1976)), and in Lake Escanaba ($7.2 - 30.6$ age 4 fish.ha⁻¹ or $1.7 - 13.3$ age 7 fish.ha⁻¹ (Serns 1982)). Based on this comparison we assume that the pikeperch stock is recruitment overfished. The smelt stock shows to date no signs of over-exploitation. Knowing that prey fish is plentiful, management experiments should be carried out to enlarge spawning stock biomass of pikeperch via strong limitations on fishing effort to enhance recruitment until the smelt stock shows signs of intensive use. We think that rationalism in management should prevail in spite of a desperate search for significant correlations, which is conform with the vision of Walters and Collie (1988) and Walters and Holling (1990), who question the use of research on environmental factors to fisheries management and who propose bold management experiments.

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REFERENCES

- Alm, G. 1952. Year class fluctuations and span of life of perch. Rep. Inst. Freshw. Res. Drottningholm 33: 17-38.

- Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J. Northw. Atl. Fish. Sci.* 8: 55-66.
- Buijse, A.D., and W.L.T. van Densen. 000. Flexibility in the onset of piscivory and growth depensation in Eurasian perch, *Perca fluviatilis* L.. (chapter 5)
- Buijse, A.D., M.R. van Eerden, W. Dekker, and W.L.T. van Densen. 1991. A trophic model for IJsselmeer (The Netherlands), a shallow eutrophic lake. p. 000-000 *In* V. Christensen, and D. Pauly [eds.] *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings No. 26.
- Buijse, A.D., and R.P. Houthuijzen. 1992. Piscivory, growth and size-selective mortality of age 0 pikeperch, *Stizostedion lucioperca* (L.). *Can. J. Fish. Aquat. Sci.* 49: 000-000.
- Buijse, A.D., L.A. Schaap, and T.P. Bult. 1992. The influence of water clarity on the catchability of six freshwater fish species in bottom trawls. *Can. J. Fish. Aquat. Sci.* 49: 000-000.
- Busch, W.-D. N., R.L. Scholl, and W.L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in Western Lake Erie, 1960-70. *J. Fish. Res. Board Can.* 32: 1733-1743.
- Carlander, K.D., and P.M. Payne. 1977. Year-class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa. 1948-74, with varied fry stocking rates. *J. Fish. Res. Board Can.* 34: 1792-1799.
- Chevalier, J.R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. *Trans. Am. Fish. Soc.* 102: 739-744.
- Clady, M.D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. *J. Fish. Res. Board Can.* 33: 1887-1893.
- Clady, M., and B. Hutchinson. 1975. Effect of high winds on eggs of yellow perch, *Perca flavescens*, in Oneida Lake, New York. *Trans. Am. Fish. Soc.* 104: 524-525.
- Craig, J.F., and C. Kipling. 1983. Reproduction effort versus the environment; case histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L.. *J. Fish Biol.* 22: 713-727.
- Craig, J.F., C. Kipling, E.D. LeCren, and J.C. McCormack. 1979. Estimates of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1967 to 1977 and some comparisons with earlier years. *J. Anim. Ecol.* 48: 315-325.
- Crowder, L.B., M.E. McDonald, and J.A. Rice. 1987. Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. *Can. J. Fish. Aquat. Sci.* 44: 141-147.
- Dekker, W. 1991. Assessment of the historical downfall of the IJsselmeer fisheries using anonymous inquiries for effort data. p. 233-240. *In* I.G. Cowx [ed.] *Catch effort sampling techniques: their application in freshwater fisheries management*. Fishing News Books, Blackwell Scientific Publications, Oxford.
- Densen, W.L.T. van. 1985. Piscivory and the development of bimodality in the size distribution of 0+ pikeperch (*Stizostedion lucioperca* L.). *J. Appl. Ichthyol.* 1: 119-131.
- Densen, W.L.T. van, W.G. Cazemier, W. Dekker, and H.G.J. Oudelaar. 1990. Management of the fish stocks in Lake IJssel, The Netherlands. p. 313-327. *In* W.L.T. van Densen, B. Steinmetz, and R.H. Hughes [ed.] *Management of freshwater fisheries. Proceedings of a symposium organized by the European Inland Fisheries Advisory Commission, Göteborg, Sweden 31 May - 3 June 1988*. PUDOC, Wageningen.

- Eerden, M.R. van, and M. Zijlstra. 1985. Aalscholvers *Phalacrocorax carbo* in de Oostvaardersplassen, 1970-85. *Limosa* 58: 137-143.
- Forney, J.L. 1971. Development of dominant year classes in a yellow perch population. *Trans. Am. Fish. Soc.* 100: 739-749.
- Forney, J.L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. *Trans. Am. Fish. Soc.* 103: 15-24.
- Forney, J.L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966-73. *J. Fish. Res. Board Can.* 33: 783-792.
- Forney, J.L. 1977. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. *J. Fish. Res. Board Can.* 34: 925-932.
- Forney, J.L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. *N. Y. Fish Game J.* 27: 105-141.
- Guma'a, S.A. 1978. The effects of temperature on the development and mortality of eggs of perch, *Perca fluviatilis*. *Freshw. Biol.* 8: 221-227.
- Hartmann, J., and S. Blank. 1989. Jahrgangsstärke (Rekrutierung) beim Barsch (*Perca fluviatilis*) des Bodensees. *Österreichs Fischerei* 42: 158-164.
- Hatch, R.W., S.J. Nepszy, K.M. Muth, and C.T. Baker. 1987. Dynamics of the recovery of the Western Lake Erie walleye (*Stizostedion vitreum vitreum*) stock. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2): 15-22.
- Henderson, B.A. 1985. Factors affecting growth and recruitment of yellow perch, *Perca flavescens* Mitchell, in South Bay, Lake Huron. *J. Fish Biol.* 26: 449-458.
- Henderson, B.A., and S.J. Nepszy. 1988. Recruitment of yellow perch (*Perca flavescens*) affected by stock size and water temperature in Lakes Erie and St. Clair, 1965-85. *J. Great Lakes Res.* 14: 205-215.
- Hennemuth, R.C., J.E. Palmer, and B.E. Brown. 1980. A statistical description of recruitment in eighteen selected fish stocks. *J. Northw. Atl. Fish. Sci.* 1: 101-111.
- Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *J. Fish. Res. Board Can.* 34: 1524-1550.
- Jones, R. 1984. Assessing the effects of changes in exploitation pattern using length composition data (with notes on VPA and cohort analysis). *FAO Fish. Tech. Pap.* 256: 118 p.
- Kallemeyn, L.W. 1987. Correlations of regulated lake levels and climatic factors with abundance of young-of-the-year walleye and yellow perch in four lakes in Voyageurs National park. *N. Am. J. Fish. Manag.* 7: 513-521.
- Kipling, C. 1976. Year class strengths of perch and pike in Windermere. *Freshw. Biol. Assoc. Annu. Rep.* 44: 68-75.
- Kokurewicz, B., 1969. The influence of temperature on the embryonic development of the perches: *Perca fluviatilis* L. and *Lucioperca lucioperca* (L.). *Zool. Pol.* 19: 47-67.
- Koonce, J.F., T.B. Bagenal, R.F. Carline, K.E.F. Hokanson, and M. Nagiec. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. *J. Fish. Res. Board Can.* 34: 1900-1909.

- LeCren, E.D. 1987. Perch (*Perca fluviatilis*) and pike (*Esox lucius*) in Windermere from 1940 to 1985: studies in population dynamics. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2): 216-228.
- LeCren, E.D., C. Kipling, and J.C. McCormack. 1977. A study of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1941 to 1966. *J. Anim. Ecol.* 46: 281-307.
- Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45: 1657-1670.
- Mills, C.A., and M.A. Hurley. 1990. Long-term studies on the Windermere populations of perch (*Perca fluviatilis*), pike (*Esox lucius*) and Arctic charr (*Salvelinus alpinus*). *Freshw. Biol.* 23: 119-136.
- Mills, E.L., and J.L. Forney. 1988. Trophic dynamics and development of freshwater pelagic food webs. p. 11-30. *In* S.R. Carpenter [ed.] *Complex interactions in lake communities*. Springer-Verlag, New York.
- Mills, E.L., J.L. Forney, and K.J. Wagner. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. p. 118-131. *In* W.C. Kerfoot, and A. Sih [ed.] *Predation. Direct and indirect impact on aquatic communities*. University Press of New England, Hannover, London.
- Nelson, W.R., and C.H. Walburg. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River reservoirs. *J. Fish. Res. Board Can.* 34: 1748-1763.
- Nielsen, L.A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *J. Fish. Res. Board Can.* 37: 11-19.
- Pepin, P. 1991. Effects of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Can. J. Fish. Aquat. Sci.* 48: 503-518.
- Peterson, I., and J.S. Wroblewski. 1984. Mortality rates of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* 41: 1117-1120.
- Pitcher, T.J., and P.J.B. Hart. 1982. *Fisheries ecology*. Croom Helm, London. 414 p.
- Raitaniemi, J., M. Rask, and P.J. Vuorinen. 1988. The growth of perch, *Perca fluviatilis* L., in small Finnish lakes at different stages of acidification. *Ann. Zool. Fennici* 25: 209-219.
- Rask, M., and P. Tuunainen. 1990. Acid-induced changes in fish populations of small Finnish lakes. p. 911-927. *In* P. Kauppi et al. [ed.] *Acidification in Finland*. Springer-Verlag, Berlin.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191: 382 pp.
- Ritchie, B.J., and P.J. Colby. 1988. Even-odd year differences in walleye year-class strength related to mayfly production. *N. Am. J. Fish. Manag.* 8: 210-215.
- Serns, S.L. 1982. Influence of various factors on density and growth of age-0 walleyes in Escanaba Lake, Wisconsin, 1958-1980. *Trans. Am. Fish. Soc.* 111: 299-306.
- Shuter, B.J., and J.F. Koonce. 1977. A dynamic model of the Western Lake Erie walleye (*Stizostedion vitreum vitreum*) population. *J. Fish. Res. Board Can.* 34: 1972-1982.
- Smith Jr., L.L. 1977. Walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations and fisheries of the Red Lakes, Minnesota, 1930-75. *J. Fish. Res. Board Can.* 34: 1774-1783.

- Staub, E., B. Büttiker, and A. Krämer. 1987. Grundlagen für Modellsimulationen zur Bewirtschaftung des Barsches (*Perca fluviatilis* L.) im Bodensee. Bundesamt für Umweltschutz, Bern. Schriftenreihe Fischerei. Nr. 46. 40 p.
- Staub, E., and A. Krämer. 1991. Grossversuch mit 28mm-Netzen zur Befischung der Wachstumsverzögerten Barschkohorte 1988. SVA/IBK. 27 p. + appendices.
- Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshw. Res. Drottningholm 55: 144-171.
- Svärdson, G., and G. Molin. 1973. The impact of climate on Scandinavian populations of the sander, *Stizostedion lucioperca* (L.). Rep. Inst. Freshw. Res. Drottningholm 53: 78-112.
- Svärdson, G., and G. Molin. 1981. The impact of eutrophication and climate on a warmwater fish community. Rep. Inst. Freshw. Res. Drottningholm 59: 142-151.
- Tarby, M.J. 1974. Characteristics of yellow perch cannibalism in Oneida Lake and the relation to first year survival. Trans. Am. Fish. Soc. 103: 462-471.
- Thorpe, J. 1977. Synopsis of biological data on the perch, *Perca fluviatilis* Linnaeus, 1758 and *Perca flavescens* Mitchill, 1814. FAO Fish. Synop. 113: 138 p.
- Treasurer, J.W. 1983. Estimates of egg and viable embryo production in a lacustrine perch, *Perca fluviatilis*. Env. Biol. Fish. 8: 3-16.
- Walters, C.J., and J.S. Collie. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45: 1848-1854.
- Walters, C.J., and C.S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71: 2060-2068.
- Willemsen, J. 1974. Vislarvenbemonstering IJsselmeer en andere snoekbaarswateren. (Fish larvae sampling Lake IJssel and other pikeperch waters). Netherlands Institute for Fishery Research. IJmuiden. 12 p. + Figs. and Tables (in dutch)
- Willemsen, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34: 1710-1719.
- Willemsen, J. 1983. Biology and management of pikeperch. Proc. 3rd. Brit. Freshw. Fish. Conf., Univ. of Liverpool. p. 115-125.
- Willemsen, J. 1985. De invloed van de visserij met fuiken op de snoekbaars- en baarsstand in het IJsselmeer (The impact of the fyke net fishery on the pikeperch and perch stock in Lake IJssel). Netherlands Institute for Fishery Research. IJmuiden. Report 85-02. 10 p. (in dutch)
- Wolfert, D.R. 1981. The commercial fishery for walleyes in New York waters of Lake Erie, 1959-1978. N. Am. J. Fish. Manag. 1: 112-126.

Appendix 1. Estimated landings and fishing mortalities of perch per age-group and year-class during a fishing season which lasted from 1 July to 15 March. Numerical abundance of age-groups in the landings were estimated by (a) taking the ratio of the landings in a specific year and the weight of market samples, and (b) the age-length key based on length frequencies of the market samples, and the number of aged fish per cm-class. Fishing mortalities were estimated using cohort analysis with input values of F_{age-7} and $older = 0.8 \text{ yr}^{-1}$ and $M = 0.2 \text{ yr}^{-1}$ for the year-classes [69] - [81]. For the year-classes [82] - [85] the mean F based on the year-classes [69] - [81] was used as input value.

a. landings in numbers $\times 1,000$; 0 means less than 500 fish caught. (number of aged fish are given in parentheses)

| age | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 |
|-------|------|-------|------|-------|-------|-------|------|------|-------|
| 1 | 3 | (2) | | | | | | | |
| 2 | | 16 | (6) | | 10 | 16 | (5) | 85 | (1) |
| 3 | 1359 | (129) | 881 | (230) | 384 | (64) | 16 | (3) | 389 |
| 4 | 769 | (189) | 1278 | (193) | 1058 | (217) | 44 | (19) | 455 |
| 5 | 235 | (36) | 584 | (130) | 769 | (328) | 44 | (4) | 260 |
| 6 | 55 | (13) | 418 | (178) | 54 | (6) | 45 | (6) | 2 |
| 7 | 21 | (9) | 22 | (2) | 122 | (16) | 28 | (4) | 97 |
| 8 | 10 | (1) | 24 | (3) | 47 | (6) | 3 | (1) | 4 |
| 9 | | | | | | | 6 | (1) | 5 |
| 10 | | | | | | | | | 5 |
| total | 2452 | (379) | 3224 | (742) | 2435 | (637) | 177 | (37) | 1328 |
| | | | | | (300) | 491 | (61) | 2273 | (445) |
| | | | | | | | | 2509 | (408) |
| | | | | | | | | | 343 |
| | | | | | | | | | (51) |

b. fishing mortality (yr^{-1})

| age | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 |
|-----|------|------|------|------|------|------|------|------|------|
| 1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.02 | 0.00 | 0.00 |
| 3 | 0.66 | 0.24 | 0.12 | 0.06 | 0.35 | 1.29 | 0.04 | 0.06 | 0.00 |
| 4 | 1.02 | 0.64 | 0.57 | 0.22 | 0.62 | 0.20 | 0.47 | 0.69 | 1.39 |
| 5 | 1.09 | 0.69 | 1.16 | 0.36 | 0.93 | 0.18 | 0.95 | 1.22 | 1.22 |
| 6 | 0.84 | 2.03 | 0.21 | | 0.01 | 1.16 | 1.05 | 1.69 | 1.00 |

Appendix 1 continued.

a. landings in numbers x 1,000; 0 means less than 500 fish caught. (number of aged fish are given in parentheses)
year-class

| age | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 |
|-------|------|-------|-----|------|------|-------|------|-------|
| 1 | | | | | | | (1) | |
| 2 | | | 39 | 53 | (6) | 110 | (20) | 56 |
| 3 | 173 | (23) | 116 | (7) | 99 | (17) | 1573 | (229) |
| 4 | 1506 | (393) | 178 | (67) | 81 | (18) | 1292 | (101) |
| 5 | 763 | (68) | 6 | (71) | 51 | (4) | 371 | (452) |
| 6 | 13 | (2) | | (16) | 5 | (6) | 68 | (80) |
| 7 | 11 | (2) | 5 | (6) | 1 | (1) | | |
| 8 | 26 | (2) | 0 | (1) | | | | |
| 9 | 4 | (4) | | | | | | |
| 10 | | | | | | | | |
| total | 2495 | (494) | 301 | (45) | 1200 | (168) | 290 | (52) |
| | | | | | 3414 | (882) | 909 | (940) |
| | | | | | | | 440 | (542) |
| | | | | | | | | 391 |
| | | | | | | | | (415) |

b. fishing mortality (yr⁻¹)

| age | | | | | | | | |
|-----|------|------|------|------|------|------|------|------|
| 1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 0.00 | 0.00 | 0.02 | 0.14 | 0.02 | 0.04 | 0.00 | 0.01 |
| 3 | 0.05 | 0.41 | 0.73 | 0.43 | 0.51 | 0.11 | 0.55 | |
| 4 | 0.90 | 2.89 | 1.66 | 0.75 | 1.12 | 1.26 | | |
| 5 | 2.32 | | 2.18 | 2.07 | 1.30 | | | |
| 6 | 0.20 | | 0.00 | 1.54 | | | | |

Appendix 2. Estimated landings and fishing mortalities of pikeperch per age-group and year-class during a fishing season which lasted from 1 July to 15 March. Numerical abundance of age-groups in the landings were estimated by (a) taking the ratio of the landings in a specific year and the weight of market samples, and (b) the age-length key based on length frequencies of the market samples, and the number of age fish per cm-class. Fishing mortalities were estimated using cohort analysis with input values of $F_{\text{age } 5 \text{ and older}} = 0.4 \text{ yr}^{-1}$ and $M = 0.2 \text{ yr}^{-1}$ for the year-classes [67] - [83]. For the year-classes [84] - [86] the mean F based on the year-classes [67] - [83] was used as input value.

a. landings in numbers $\times 1,000$; 0 means less than 500 fish caught. (number of aged fish are given in parentheses)

| age | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 |
|-------|-------------|-----------|------------|------------|-----------|-----------|------------|-----------|------------|-----------|
| 1 | | | 8 (59) | | | | 1 (1) | | 40 (33) | |
| 2 | 308 (664) | 99 (767) | 1540 (622) | 909 (622) | 428 (294) | 126 (171) | 1417 (316) | 111 (99) | 1035 (666) | 474 (207) |
| 3 | 55 (380) | 22 (9) | 125 (25) | 244 (25) | 52 (80) | 36 (8) | 200 (195) | 8 (5) | 128 (56) | 432 (300) |
| 4 | 5 (2) | 2 (2) | 17 (13) | 17 (13) | 4 (1) | 4 (4) | 16 (10) | 2 (1) | 56 (39) | 26 (26) |
| 5 | | | 3 (4) | | 5 (5) | 2 (1) | | 3 (2) | 12 (12) | 2 (6) |
| 6 | 1 (1) | | | 1 (1) | | | 12 (8) | | 2 (6) | 1 (2) |
| 7 | | | 1 (1) | | 5 (2) | 1 (1) | 2 (2) | 0 (1) | 2 (4) | 4 (11) |
| 8 | | | | 1 (1) | | | | 0 (1) | 2 (4) | 4 (2) |
| 9 | | | | | | | 0 (3) | | | |
| 10 | | | 1 (1) | | | | 2 (6) | | 13 (1) | 3 (2) |
| total | 369 (1,047) | 124 (778) | 1696 (725) | 1172 (359) | 494 (382) | 169 (185) | 1650 (541) | 125 (108) | 1290 (823) | 945 (557) |

b. fishing mortality (yr^{-1})

| age | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 |
|-----|------|------|------|------|------|------|------|------|------|------|
| 1 | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 |
| 2 | 1.62 | 1.36 | 2.20 | 1.32 | 1.71 | 1.17 | 1.72 | 1.81 | 1.45 | 0.58 |
| 3 | 2.17 | 1.59 | 1.58 | 2.35 | 1.14 | 1.48 | 1.59 | 0.57 | 0.69 | 2.12 |
| 4 | 1.88 | | 1.05 | 1.67 | 0.25 | 0.56 | 0.46 | 0.33 | 0.75 | 0.79 |

Appendix 2 continued.

a. landings in numbers x 1,000; 0 means less than 500 fish caught. (number of aged fish are given in parentheses)

| age | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 |
|-------|---------|---------|----------|----------|-----------|-----------|-----------|---------|-----------|-----------|
| 1 | 4 (3) | 11 (11) | 56 (173) | 36 (173) | 3 (4) | 38 (101) | 90 (100) | 10 (8) | 148 (719) | 0 (2) |
| 2 | 21 (21) | 6 (19) | 5 (6) | 5 (6) | 99 (258) | 379 (221) | 19 (15) | 7 (36) | 14 (36) | 200 (607) |
| 3 | 2 (5) | 2 (5) | 2 (5) | 2 (5) | 8 (13) | 14 (22) | 6 (29) | 1 (2) | | |
| 4 | 1 (1) | 1 (2) | 1 (2) | 3 (2) | 4 (3) | 1 (4) | 1 (3) | | | |
| 5 | 1 (2) | | | 0 (1) | 0 (1) | 1 (2) | | | | |
| 6 | 1 (2) | | | 0 (1) | 0 (3) | | | | | |
| 7 | | | | | | | | | | |
| 8 | | | | | | | | | | |
| 9 | | | | | | | | | | |
| 10 | 0 (2) | | | | | | | | | |
| total | 29 (34) | 18 (33) | 63 (186) | 43 (62) | 115 (276) | 433 (350) | 116 (147) | 18 (46) | 162 (755) | 200 (609) |

b. fishing mortality (yr⁻¹)

| age | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|-----|------|------|------|------|------|------|------|------|------|------|
| 1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 0.12 | 0.79 | 1.87 | 1.33 | 1.75 | 2.96 | 1.30 | 0.65 | 2.06 | |
| 3 | 1.53 | 1.71 | 0.81 | 0.64 | 0.62 | 1.79 | 1.19 | 1.69 | | |
| 4 | 0.41 | 0.00 | | 0.00 | 0.00 | 0.00 | 1.98 | | | |

Chapter 4

PISCIVORY, GROWTH AND SIZE-SELECTIVE MORTALITY OF AGE 0 PIKEPERCH, *STIZOSTEDION LUCIOPERCA* (L.).

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ABSTRACT

Year-class strength of pikeperch (*Stizostedion lucioperca*), indexed as the age 0 abundance in trawl surveys, varied 300-fold in the northern part of Lake IJssel, The Netherlands, over the period 1966-1989. Both mean length and year-class strength of age 0 pikeperch in November were correlated strongly with mean summer temperature. Depending on the environmental conditions, especially water temperature and availability of food) the unimodal length frequency distribution of age 0 pikeperch developed into a positively skewed, bimodal or negatively skewed distribution towards the end of the summer. Strong year-classes were characterised by larger mean lengths, and a negatively skewed frequency distribution, while weak year-classes were smaller and positively skewed. Stomach contents consisted of zooplankton and macrofauna for the smaller fish and of age 0 smelt (*Osmerus eperlanus*) for the larger pikeperch (>10 cm). Body energy content increased with fish length and differences in proximate analysis were more pronounced later in the season. The condition of non-piscivorous age 0 pikeperch was low and decreased over time, while that of piscivorous pikeperch increased over time. The onset of piscivory, favoured by high temperatures during summer, has a direct positive effect on the growth and survival of age 0 pikeperch.

INTRODUCTION

Year-class strength (YCS) of pikeperch *Stizostedion lucioperca* (L.), indexed as the average number of age 0 fish per standard trawl haul during autumn surveys, varied 20-fold in Lake IJssel over the period 1966-75. The abundance of age 0 pikeperch during these autumn trawl surveys was highly correlated with the commercial landings of the same year-classes and therefore can be considered as a reliable measure of pikeperch recruited to the fishery (Willemsen 1977). Although the positive influence of high summer temperatures is often considered the principal factor contributing towards strong year-class formation of percids (e.g. Koonce et al. 1977; Willemsen 1983; LeCren 1987), the effect of temperature on survival is rarely discussed (Busch et al. 1975; Clady 1976). According to Hokanson (1977), the physiological optimum for pikeperch is 27.3°C and the growth optimum is 28-30°C. Warm summers in Lake IJssel always resulted in a faster growth of age 0 pikeperch, probably because these optimum temperatures are never reached (Willemsen 1983), which suggests that temperature affects survival indirectly through enhanced growth.

In Lake IJssel, strong year-classes of pikeperch are in general characterised by a mean length of over 14 cm by the end of their first growing season (Willemsen 1977, 1983). The more than two-fold difference between years in mean length attained in autumn (Willemsen 1983) might be explained by higher summer temperatures, but van Densen (1985) suggested that it was the switch towards a piscivorous feeding mode, which enhanced growth. In particular the largest members of a cohort would profit from this switch. Size-related differential prey availability may result in the divergences in length over time among individuals in the same age-class (Keast and Eadie 1985), and bimodality (DeAngelis and Coutant 1982). Bimodality in size-distributions of one cohort has been described for a number of piscivorous species including largemouth bass (*Micropterus salmoides*) (Aggus and Elliott 1975; Shelton et al. 1979; Timmons et al. 1980), Eurasian perch (*Perca fluviatilis*) (Chodorowski 1975), walleye (*Stizostedion vitreum*) (McIntyre et al. 1987) and pikeperch (van Densen 1985).

The most important prey fish for age 0 pikeperch in Lake IJssel is European smelt, *Osmerus eperlanus* (Willemsen 1977). Smelt spawn in March and April about 1 month prior to pikeperch (Willemsen 1977) and therefore have the potential to be readily available as preferred prey for pikeperch when they are large enough to switch to a piscivorous diet. Mean summer temperature had no significant effect on smelt growth in Tjeukemeer (W. Mooij pers.comm.) and Lake IJssel (Brasseur 1990). However, above 15°C the growth rate of smelt was lower than that of planktivorous pikeperch in Tjeukemeer (W. Mooij

pers.comm.). Thus, it seems likely that at high temperatures planktivorous age 0 pikeperch may surpass age 0 smelt in length and become piscivorous.

Further, abundance of pikeperch larvae in May and June did not correlate with their abundance during autumn trawl surveys (Willemsen 1977). This lack of correlation could be the result of inadequate sampling of larvae or simply because larvae abundance does not determine YCS. The object of this study therefore was to investigate if the switch in feeding behaviour from zooplankton and macrofauna to fish in the summer influences year-class formation of pikeperch. It is hypothesised that due to the non-availability of prey fish smaller fish of the same cohort are in a poorer condition resulting in size-selective mortality of the smaller fish. Age 0 pikeperch were therefore also analysed for their condition in terms of energy content per unit body weight.

MATERIAL AND METHODS

Study area

A description of the chemical and physical characteristics of Lake IJssel, a shallow eutrophic 182,000 ha freshwater lake (52°45'N, 5°20'E), is given in Willemsen (1977) and Buijse et al. (000). Water temperatures (± 0.1 °C) in Lake IJssel were measured daily and expressed as degree-days above 14°C.

Surveys

Data used in this study originate from trawl surveys in the northern part of Lake IJssel in 1966-1989. A routine lake-wide survey programme has been carried out in August and November 1966-1986, using a bottom trawl (cod-end 20-mm stretched mesh). A description of the sampling sites and the trawl is given by Buijse et al. (000). In 1987-1989 sampling was intensified; abundance and length of pikeperch and of smelt were also recorded in June (cod-end 2-mm stretched mesh) and September, and the number of sampling sites was increased to 15 (unpublished data).

Fish were sorted by species on deck, and weighed to the nearest 0.1 kg. Total length of individual fish was measured to the nearest cm. During surveys in June, age-0 fish were preserved with 4% formalin for later identification and measurement to the nearest 0.5 cm in the laboratory. To estimate the mean abundance of a fish species, indices were calculated by taking the geometric mean of the catches (adding 1). Since the ropes of the 2 mm trawl are about half the length of those of the 20 mm trawl, catches in the 2 mm trawl were doubled to be comparable with catches made by the 20 mm trawl. During the August and September surveys in 1988, age 0 pikeperch were collected and

frozen for later determination of their energy content, dry weight, and stomach contents.

Lab methods

Each 1-cm size-class of age 0 pikeperch retained for stomach analysis was weighed to the nearest 0.1 mg and frequencies of occurrence of prey in the stomachs was recorded. Subsequently the fish were cut into 1-cm pieces, freeze dried and reweighed. Calorimetric analysis required samples of at least 30 g (wet weight), therefore the two largest size-classes, 14 and 15 cm in August and 16 and 17 cm in September, were pooled but the smallest size-classes, 4 and 5 cm, could not be analysed due to weight restrictions. All the freeze-dried samples were ground separately and the dry weight of each sample was measured by weighing a subsample of about 2 g, drying it at 105°C for 4 h, and reweighing to a precision of 0.1 mg. The remainder was used to determine the energy content with an adiabatic bomb-calorimeter (IKA-Kalorimeter C400). Both dry weight and energy content measurements were carried out in duplicate. If the energy content of the duplicate determinations differed by more than 2%, the analysis was repeated using new samples. Fat percentages were estimated indirectly by assuming 39.5 kJ.g⁻¹ fat and 23.5 kJ.g⁻¹ protein (Brafield 1985) and using $\log_e \text{ASH} = 3.496 * \log_e \text{TL} - 9.557$ where ASH = absolute ash weight (g) and TL = total length (cm) as measured for 2 to 13 cm age 0 pikeperch (n=49; r²=0.997).

$$\text{fat} = \left(\frac{\frac{EC}{AFF} - 23.5}{39.5 - 23.5} \right) * AFF * DW \quad (\% \text{ of FW})$$

where:

EC = energy content (kJ.g⁻¹ dry wt)

ASH = ash weight (g)

FW = fresh weight (g)

DW = dry weight (% of fresh weight)

AFF = ash-free fraction of dry weight, $1 - \text{ASH} * 100.(\text{FW} * \text{DW})^{-1}$ (-)

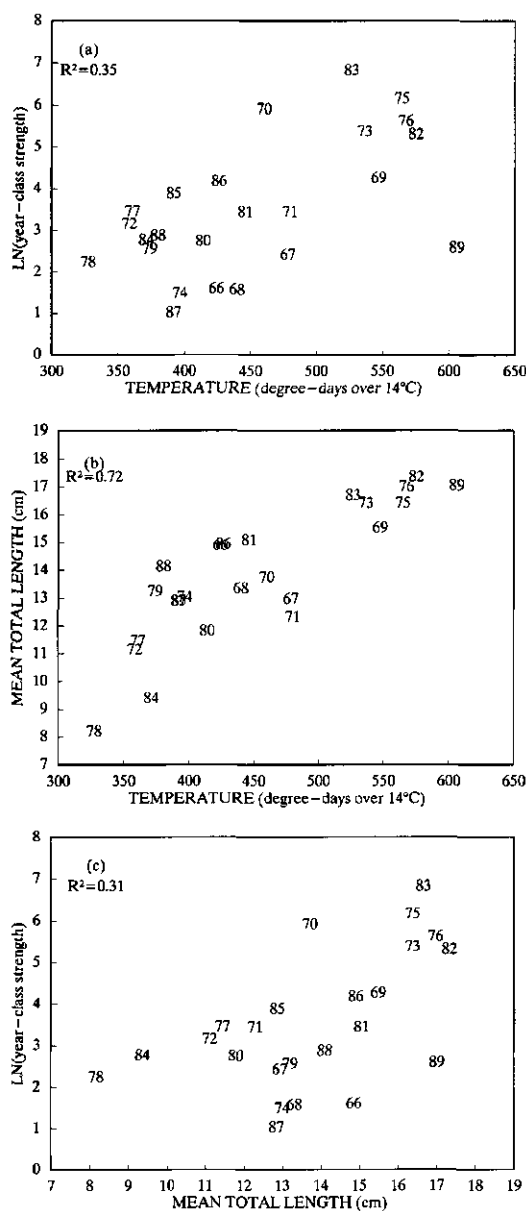


Fig. 1. Year-class strength (a) and mean length (b) of age 0 pikeperch versus the water temperature (year-sum of degree days over 14°C), and year-class strength versus mean length (c) based on November trawl surveys at the northern part of Lake IJssel over the period 1966-1989. Year-class strength is given as \log_e number caught per hour trawling (geometric mean of 3 to 8 hauls). $N = 24$; all correlations are significant at $p < 0.01$.

RESULTS

Log transformed YCS index and mean length of age 0 pikeperch were positively correlated with water temperature (Figs. 1a and 1b) and with each other (Fig. 1c). The mean length of age 0 fish in the autumn trawl surveys varied between 8.2 and 17.3 cm, whilst YCS varied between 2.7 and 903 age 0 pikeperch per hour trawling. Water temperature varied between 327 and 606 degree-days over 14°C. Over the period 1966-1989 water temperature explained 72% of the variation in length and 35% of the variation in YCS. Growth was the highest in the warm summer of 1989, but the YCS was much lower than expected.

Table 1. Descriptive statistics of age 0 pikeperch, smelt and water temperature (cumulative degree days over 14°C) in the northern part of Lake IJssel during 4 sampling periods in 1987, 1988 and 1989. N = number caught per hour trawling (geometric mean of 15 hauls of 10 minutes); TL = mean total length; SD = standard deviation of the length; SKNS = skewness; * $p < 0.05$, *** $p < 0.001$ = significance of skewness¹⁾

| | pikeperch | | | | smelt | | | | |
|----------------------|-----------|------------|------------|--------------|-------|------------|------------|--------------|-----------------|
| | N | TL (cm) | SD (cm) | SKNS (cm) | N | TL (cm) | SD (cm) | SKNS (cm) | temp. (°C.d) |
| 1987 | | | | | | | | | |
| 29 June - 3 July | 36 | 2.2 | 0.66 | 0.17 | 3632 | 3.6 | 0.57 | -0.17 | 46 |
| 17-21 August | 24 | 6.0 | 1.17 | 0.98*** | 3561 | 6.2 | 0.66 | -0.19 | 256 |
| 7-10 September | 39 | 7.2 | 2.06 | 1.96*** | 1607 | 6.8 | 0.50 | -0.43 | 342 |
| 9-12, 17 November | 3 | 8.3 | 2.48 | 2.21*** | 378 | 7.7 | 0.72 | -0.12 | 392 |
| 1988 | | | | | | | | | |
| 27-30 June | 22 | 2.9 | 0.80 | 0.94*** | 24089 | 3.9 | 0.64 | 0.00 | 97 |
| 15-18, 22, 23 August | 56 | 8.8 | 2.11 | 0.14 | 10275 | 5.8 | 0.60 | 0.02 | 289 |
| 12-16 September | 68 | 11.5 | 2.51 | -0.33* | 9270 | 6.0 | 0.53 | 0.13 | 368 |
| 14-17, 23 November | 10 | 14.1 | 2.40 | -0.86* | 10992 | 6.5 | 0.56 | 0.41 | 380 |
| 1989 | | | | | | | | | |
| 19-22 June | 24 | 3.3 | 0.85 | -0.34 | 6869 | 3.6 | 0.59 | 0.32 | 121 |
| 14-17, 21, 22 August | 237 | 12.2 | 2.18 | -0.51*** | 2525 | 6.8 | 0.64 | 0.02 | 418 |
| 11-15 September | 188 | 15.7 | 2.70 | -0.94*** | 2542 | 7.6 | 0.63 | 0.25 | 538 |
| 13-16, 20 November | 10 | 17.0 | 3.26 | -0.63 | 2385 | 8.1 | 0.76 | 0.47 | 606 |

¹⁾ Total numbers of age 0 pikeperch caught during one survey were used to estimate standard deviation, skewness, and the significance of the skewness. Those numbers differ from numbers per hour trawling, because total sampling was 2.5 hr and geometric means were calculated.

The length frequency (LF) distributions of age 0 pikeperch during the growing season in 1987-1989 illustrated the possible variation in development in size under varying environmental conditions. These three years covered by chance the range in water temperatures observed during long-term recording in Lake IJssel (Fig. 1b and 1c). Both 1987 and 1988 were cold, while 1989 was

extremely warm. Growth was slowest in 1987, intermediate in 1988 and fastest in 1989. In August, September and November 1987 LF-distributions were significantly positively skewed (Fig. 2 and Table 1). In June 1988 LF-distribution was positively skewed, but by mid August it showed bimodality, although the negative kurtosis which is an indication for bimodality (Sokal and Rohlf 1981) was not significant (kurtosis = -0.54, $p < 0.2$), with both modi of similar height. In September and November, the importance of the left modus had declined, resulting in a negatively skewed distribution. In 1989 LF-distributions were already negatively skewed in August and September.

The abundance, mean length, standard deviation and skewness in August and November 1966-1989 are given in Table 2. Out of 18 years, positively skewed distributions in August were observed in six years, and negatively skewed distributions in 2 years. Skewness (SKNS) was inversely related to mean length (TL) in August ($n=17$, $r=0.63$, $p < 0.01$, $SKNS = -0.23 * TL + 2.45$) excluding 1967, when numbers caught were small. Towards November the number of negatively skewed distribution increased to 9 out of 24 years.

Food items in the stomachs of age 0 pikeperch were zooplankton, chironomids, *Neomysis integer* and fish (age 0 smelt or indiscernible). In 1988, the diet of fish larger than 10 cm was exclusively fish (Table 3). A clear difference in the proportion of piscivores between years was observed in August (Fig. 2). In August 1987 only 11% was piscivorous, while in 1989 almost all (86%) were piscivorous. The situation in August 1988 was intermediate (68%) with the right mode representing the piscivores. In September 1988 the relative number of piscivorous pikeperch was higher (88%) than in August 1988.

Abundance of age 0 smelt, which was the most important prey fish for age 0 pikeperch, was 10 to 1000 times higher than age 0 pikeperch in the trawl catches (Table 3). Abundance of age 0 smelt was lowest in 1987, intermediate in 1989 and highest in 1988. Growth of age 0 smelt was slowest in 1988. Degree-days over 14°C were similar in the cooler years 1987 and 1988, but much higher in 1989, which was the warmest summer since the beginning of the survey in 1966. In 1988 the rate of warming was higher at the beginning of the season than in 1987.

The abundance of age 0 pikeperch in June was highest in 1987, whereafter the abundance was always lower than in 1988 and 1989 (Table 1). Abundance was high in August and September 1989, which pointed to a strong year-class. This was not corroborated by the catches in November. Differences in abundance of age 0 pikeperch in Lake IJssel in the years 1987 to 1989 were not consistent within years. The catches did not decline throughout time and gave as such no insight in mortality rates of age 0 pikeperch. The lack of decline in the catches throughout time was probably due to unknown variation in

horizontal distribution patterns and to the effect of varying water clarity on the catchability of pikeperch at the time of sampling.

The mean body weight per length-class was calculated by dividing the total sample weight by the number of pikeperch analysed in that length-class (Table 3). Based on these data the length-weight relationship for age 0 pikeperch was $W=0.00385 \cdot L^{3.29}$ where W = total weight (g) and L = total length (cm). Total body weight varied between 0.4 g for 4 cm and 28.5 g for 15 cm pikeperch in August and between 0.8 g for 5 cm and 43.0 g for 17 cm pikeperch in September.

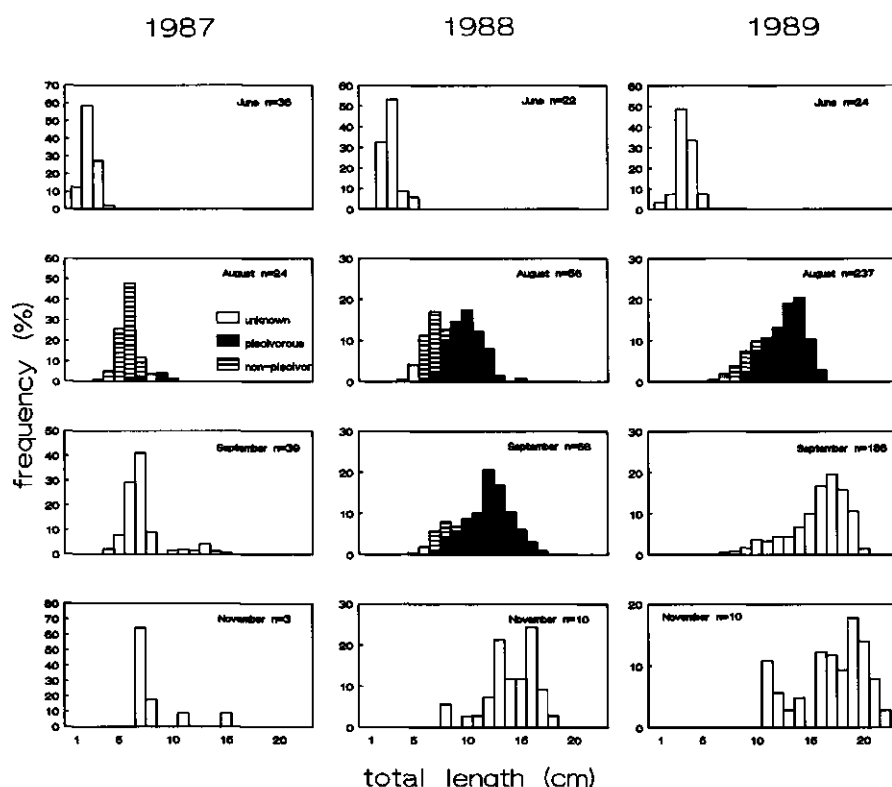


Fig. 2. Length frequency distribution of age 0 pikeperch in the northern part of Lake IJssel in June, August, September and November 1987-1989. Food items per size-class of pikeperch were only recorded in August 1987-1989 and September 1988. N = number caught per hour trawling (geometric mean of 15 hauls of 10 minutes).

Table 2. Descriptive statistics of age 0 pikeperch in the northern part of Lake IJssel in August and November 1966-89. N = number caught per hour trawling (geometric mean based on 3 to 8 hauls); TL = mean total length; SD = standard deviation; SKNS = skewness; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ = significance of skewness¹⁾. No data were collected in August in 1974, 1984-1986. Blank data for SD and SKNS means numbers caught were too low for calculations.

| year | August | | | | November | | | |
|--------------------|--------|------------|------------|----------|----------|------------|------------|----------|
| | N | TL (cm) | SD (cm) | SKNS | N | TL (cm) | SD (cm) | SKNS |
| 1966 | 6 | 9.6 | 1.20 | -0.75 | 5 | 14.9 | 1.40 | 0.12 |
| 1967 | 2 | 7.2 | 1.13 | -3.15 | 11 | 12.9 | 2.17 | -0.14 |
| 1968 | 1 | 8.5 | | | 5 | 13.3 | 2.73 | 0.84 |
| 1969 | 45 | 10.3 | 1.60 | -0.21 | 69 | 15.5 | 3.37 | -0.41 |
| 1970 | 131 | 8.5 | 1.30 | -0.20 | 362 | 13.7 | 1.92 | -0.68*** |
| 1971 | 151 | 10.5 | 1.98 | 0.42* | 30 | 12.3 | 2.79 | 0.18 |
| 1972 | 1 | 9.0 | 1.46 | | 23 | 11.1 | 2.19 | -0.10 |
| 1973 | 149 | 9.3 | 1.13 | 0.42* | 212 | 16.4 | 2.21 | -0.98*** |
| 1974 | | | | | 4 | 13.0 | 2.88 | 2.13* |
| 1975 | 37 | 10.5 | 1.47 | 0.73* | 464 | 16.4 | 2.00 | -0.63*** |
| 1976 | 24 | 11.6 | 1.88 | 0.51 | 273 | 17.0 | 2.05 | -0.47*** |
| 1977 | 10 | 10.3 | 1.06 | 0.11 | 31 | 11.0 | 2.38 | -0.03 |
| 1978 | 80 | 7.1 | 0.89 | 1.73*** | 9 | 8.2 | 1.20 | -0.92* |
| 1979 | 28 | 8.7 | 2.11 | 0.29 | 13 | 13.2 | 1.35 | 0.50 |
| 1980 | 11 | 7.3 | 1.39 | 0.95** | 15 | 11.8 | 2.50 | -0.74 |
| 1981 | 44 | 10.1 | 1.57 | -0.09 | 31 | 15.0 | 1.99 | -0.11 |
| 1982 | 115 | 12.6 | 1.73 | -0.28* | 198 | 17.3 | 2.12 | -0.39** |
| 1983 | 92 | 10.1 | 1.39 | -0.09 | 903 | 16.7 | 1.93 | -0.53*** |
| 1984 | | | | | 16 | 9.4 | 1.84 | 0.93* |
| 1985 | | | | | 47 | 12.9 | 2.69 | -0.41 |
| 1986 | | | | | 64 | 14.9 | 1.89 | -0.40* |
| 1987 ²⁾ | 23 | 6.2 | 1.21 | 1.45*** | 3 | 12.8 | 2.79 | -1.07* |
| 1988 ²⁾ | 24 | 8.5 | 2.17 | -0.12 | 17 | 14.4 | 1.82 | -0.45 |
| 1989 ²⁾ | 181 | 12.6 | 1.92 | -0.54*** | 13 | 16.9 | 3.35 | -0.56 |

¹⁾ Total numbers of age 0 pikeperch caught during one survey were used to estimate standard deviation, skewness, and the significance of the skewness. Those numbers differ from numbers per hour trawling, because the number of hauls and the duration of the hauls varied.

²⁾ Descriptive statistics for these years differ from Table 1. For reasons of comparison with previous years a smaller number of sampling sites was selected for calculations than in Table 1.

Dry weight, expressed as percentage of fresh weight, increased with length and varied between 19.0% and 24.0% (Table 3). Dry weight for all length-classes, except for 7 cm pikeperch, were similar in August and September. Energy content per unit dry weight of the total body increased with length (Fig. 3, Table 3). In August energy content varied 5.7% between 20.5 kJ.g⁻¹ dry wt for 6 and 7 cm pikeperch and 21.7 kJ.g⁻¹ dry wt for 14 to 15 cm pikeperch. In September energy content varied 13.2% between 19.8 kJ.g⁻¹ dry wt for 7 cm pikeperch and 22.6 kJ.g⁻¹ dry wt for 13 and 14 cm pikeperch. The percentage of fat estimated increased from 0.1% for planktivores to 3.5% for over 12 cm piscivores in September (Fig. 3, Table 3). The negative value for 7 cm pikeperch in September is probably the consequence of the indirect method of

calculation. From August to September both the energy content and the fat percentage of the total body had declined for pikeperch under over 9 cm, and increased for larger pikeperch.

Based on data from van Densen (1985), the ratio between predator size and maximum prey size for age 0 pikeperch and smelt was taken as 1.6. To characterise the availability of smelt for age 0 pikeperch, lengths of smelt were multiplied by this ratio following the method of Shelton et al. (1979). The LF-distributions of pikeperch and the availability of smelt are displayed in Fig. 4. A clear difference among the years was observed. In 1987 only a small part of the smelt was available for pikeperch so growth of pikeperch was stunted except for a few who were capable of eating smelt. The converse pattern was found in the warm year of 1989 when almost all pikeperch became piscivorous. An intermediate situation was displayed in 1988 and the availability corresponds with the stomach contents (Fig. 1 and Table 3).

Table 3. The number of age 0 pikeperch analysed, percentage of empty stomachs, frequency of occurrence of food items in stomachs as a percentage of fish with full stomachs, mean fresh weight of pikeperch, dry weight (% of fresh weight), energy content (g^{-1} dry weight) and fat weight (% of fresh weight) for different length-classes in the northern part of Lake IJssel, August and September 1988. zoopl = zooplankton; chiro = chironomids; Neomy = *Neomysis integer*.

| period | length-class (cm) | number | empty (%) | zoopl (%) | chiro (%) | Neomy (%) | fish (%) | fresh weight (g) | dry weight (%) | energy content (kJ) | fat weight (%) |
|-----------|----------------------|--------|--------------|--------------|--------------|--------------|-------------|------------------------|----------------------|---------------------------|----------------------|
| August | 6 | 40 | 33 | 22 | - | 85 | 7 | 1.4 | 19.6 | 20.5 | 0.2 |
| | 7 | 44 | 36 | 14 | 4 | 68 | 14 | 2.2 | 19.8 | 20.5 | 0.5 |
| | 8 | 32 | 56 | - | - | 21 | 79 | 3.4 | 19.4 | 20.6 | 0.8 |
| | 9 | 13 | 38 | - | - | - | 100 | 5.9 | 19.7 | 21.0 | 0.7 |
| | 10 | 12 | 58 | - | - | - | 100 | 7.9 | 20.6 | 21.3 | 1.3 |
| | 11 | 12 | 8 | - | - | - | 100 | 10.2 | 21.3 | 21.6 | 1.9 |
| | 12 | 8 | 63 | - | - | - | 100 | 13.5 | 21.6 | 21.5 | 1.9 |
| | 13 | 3 | 33 | - | - | - | 100 | 17.1 | 22.6 | 21.3 | 1.7 |
| | 14-15 | 2 | 50 | - | - | - | 100 | 23.6 | 23.6 | 21.7 | 2.4 |
| | | | | | | | | | | | |
| September | 7 | 25 | 36 | - | - | 81 | 19 | 2.2 | 19.0 | 19.8 | -0.1 |
| | 8 | 20 | 35 | - | - | 54 | 54 | 3.4 | 19.4 | 20.0 | 0.2 |
| | 9 | 19 | 32 | - | - | 15 | 85 | 5.2 | 19.6 | 20.9 | 1.2 |
| | 10 | 12 | 42 | - | - | - | 100 | 7.9 | 20.4 | 21.7 | 1.8 |
| | 11 | 5 | 80 | - | - | - | 100 | 10.1 | 21.3 | 22.1 | 2.6 |
| | 12 | 6 | 33 | - | - | - | 100 | 13.8 | 22.0 | 22.2 | 2.6 |
| | 13 | 6 | 50 | - | - | - | 100 | 17.5 | 22.7 | 22.6 | 3.4 |
| | 14 | 5 | 60 | - | - | - | 100 | 22.6 | 23.2 | 22.6 | 3.4 |
| | 15 | 3 | 100 | - | - | - | - | 28.2 | 23.9 | 22.5 | 3.2 |
| | 16-17 | 3 | 33 | - | - | - | 100 | 38.3 | 24.0 | 22.5 | 3.4 |

DISCUSSION

We assume that two processes play a key-role in the population dynamics of age 0 pikeperch during summer. First, differential growth between the non-piscivorous and the piscivorous, and second, size-selective mortality of the

smaller non-piscivorous individuals. Depending on the environmental conditions (water temperature, availability of smelt) both processes can modify the initial LF-distribution in a particular way. In a cooler year like 1987, only a few pikeperch were capable of switching to piscivory, which resulted in a stunted population of non-piscivores with a few larger piscivores, and the LF-distribution remained positively skewed. The non-piscivores probably have a higher mortality rate, as could be inferred from the diminishing importance of the left mode in the LF-distribution in 1988. In the warmer year of 1989, only a few pikeperch were not capable of switching to piscivory causing a negatively skewed distribution (Table 1).

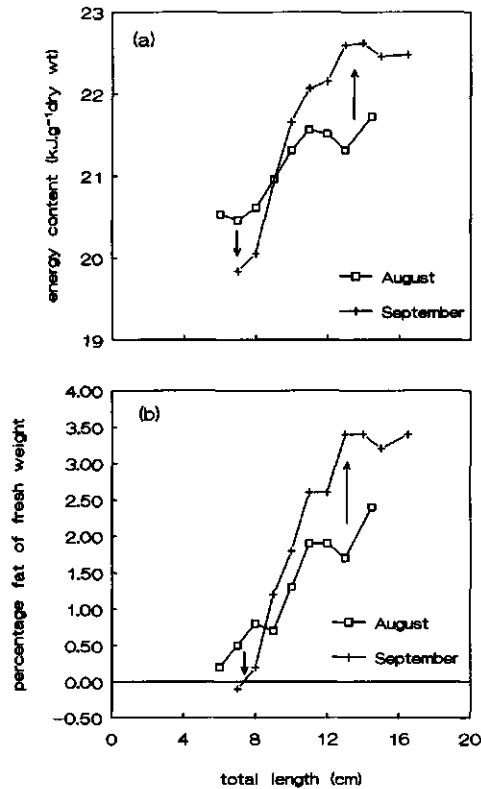


Fig. 3. Energy content (kJ.g⁻¹ dry wt) and fat weight (% of fresh weight) of age 0 pikeperch in the northern part of Lake IJssel in August and September 1988. Arrows indicate the decrease in condition of small fish and the increase in condition of larger fish.

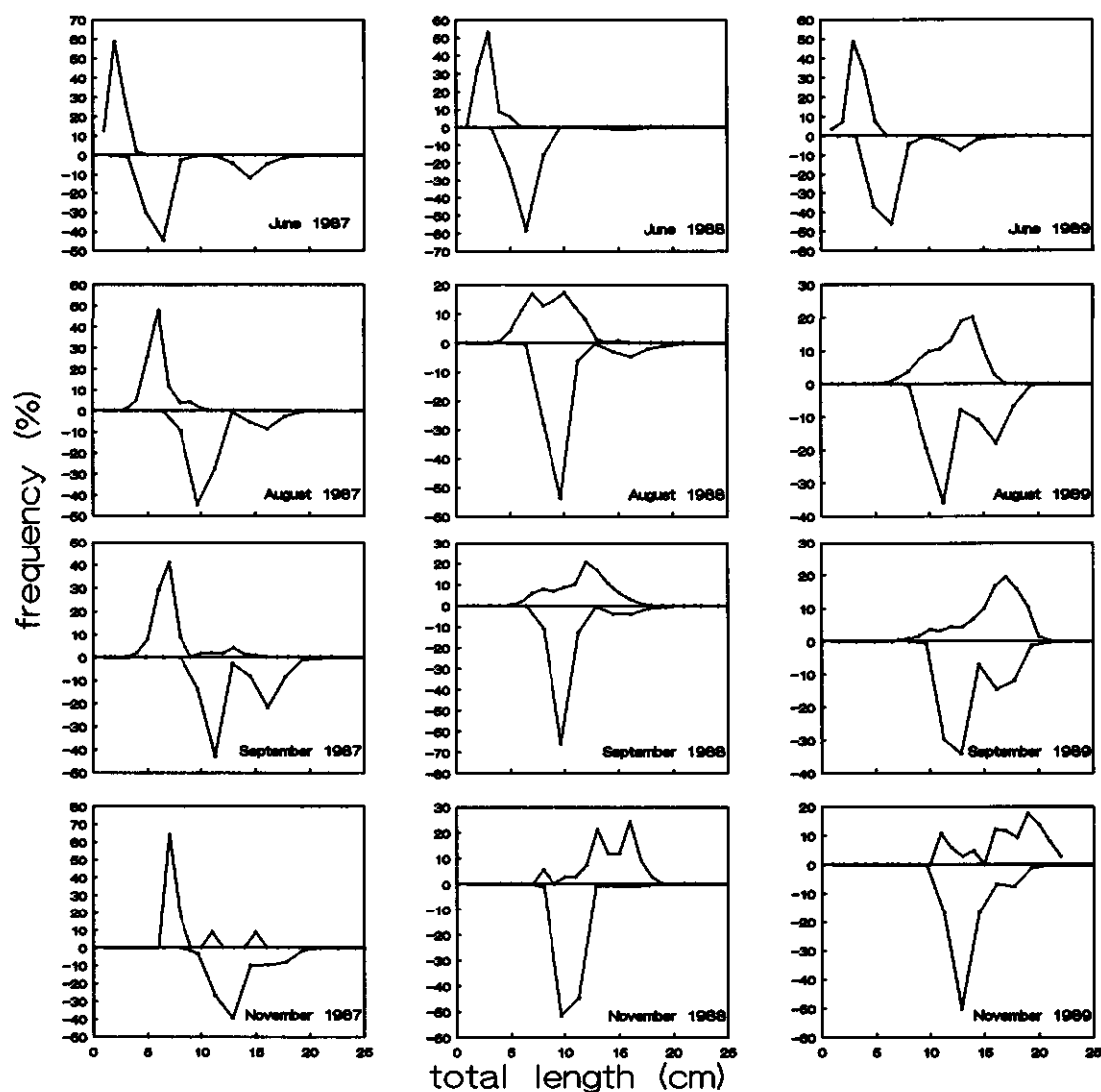


Fig. 4. Length frequencies of age 0 pikeperch (above the X-axis) and length frequencies of smelt (below the X-axis), whereof the total lengths were multiplied by 1.6 (predator: maximum prey ratio) to represent smelt available for predation in the northern part of Lake IJssel in June, August, September and November 1987 - 1989. Smelt which can be preyed upon by a certain size-class of pikeperch are all those which are straight below and to the left of that size-class.

Theoretically, the declining importance of the left modus in the LF-distribution could not only result from size-selective mortality favouring the larger piscivores similar to that found for pikeperch in another Dutch lake (van

Densen 1985) and largemouth bass (Shelton et al. 1979; Timmons et al. 1980), but also result from accelerated growth of the smaller individuals. The poor condition of the smaller non-piscivorous individuals, to our opinion, falsifies the hypothesis of accelerated growth. Further, in the period August - September 1987 the increase in modal length of the smaller non-piscivores was only 1 cm (6-7 cm), whereas in 1989 the increase in modal length of the larger piscivores was 3 cm (14-17 cm). Size-selective mortality is further exhibited by the positive correlation between mean length and abundance of age 0 pikeperch by the end of the first growing season. A notable exception was the year-class 1989, which displayed the largest growth of pikeperch. Therefore the strongest year-class was expected. Catches were, however, low in November 1989, which was probably due to unfavourable sampling conditions.

The onset of piscivory is favoured by high temperatures during summer. To be able to ingest smelt, which is the most important food item for age 0 pikeperch in Lake IJssel, a certain ratio must exist (1.6) between prey size and predator size. Since pikeperch profit from high summer temperatures, while smelt do not, a warm summer will result in a faster growth of the predator. Total degree-days over 14°C did not differ between 1987 and 1988, but was much higher in 1989, which was reflected in the faster growth of pikeperch. The enhanced growth of age 0 pikeperch in 1988 compared to 1987 was due to more age 0 pikeperch were able to switch towards piscivory in 1988. A warmer spring had resulted in a larger mean length of age 0 pikeperch in 1988 by the end of June, and the stunted growth of smelt during the summer of 1988 facilitated the onset of piscivory and rendered smelt more available to predation during the rest of the season. The difference in growth of age 0 smelt between 1987 and 1988 was probably caused by density-dependent processes; the density of age 0 smelt was about six times higher in 1988 than in 1987. Smelt manifest density-dependent growth dictated by availability of zooplankton in other Dutch lakes (van Densen and Vijverberg 1982).

As demonstrated for pikeperch, the onset of piscivory is important for the condition and survival of largemouth bass (Wicker and Johnson 1987). Age 0 largemouth bass in the 10- to 15-cm length groups were emaciated and in poor condition compared to those larger than 17 cm (Adams et al. 1982; Shelton et al. 1979). High mortality periods coincided with diet shifts towards piscivory meaning that year-class strength should not be estimated until this bottleneck has been passed (Wicker and Johnson 1987). The explanation given for stunted growth and heavy mortality of largemouth bass is a low ratio of available prey to predator biomass (Timmons et al. 1980; Wicker and Johnson 1987). There is, however, between largemouth bass and pikeperch a difference in timing with respect to their prey. Largemouth bass spawn prior to their prey (Keast 1985; Keast and Eadie 1985). Prey fishes can, however, outgrow the vulnerable size-

range. Small age 0 largemouth bass shifted from a diet comprised of zooplankton, aquatic insects and larval fish in July to one without fish in September when prey fish became too large to handle, while large age 0 fish remained piscivorous (Keast and Eadie 1985). The importance of early spawning of largemouth bass compared to that of shad (*Dorosoma petenense*, *D. cepedianum*) for recruitment has also been demonstrated with a predator-prey model by Adams and DeAngelis (1987).

Two theories exist concerning size-selective mortality due to natural causes. The first theory deals with exhaustion through a lack of energy reserves. Winter mortality is size-selective, because energy reserves are less in smaller contemporaries. Larger contemporaries of yellow perch, *Perca flavescens*, (Post and Evans 1989), smallmouth bass, *Micropterus dolomieu*, (Oliver et al. 1979), largemouth bass (Adams et al. 1982; Aggus and Elliott 1975) survived their first winter better than the smaller ones. The second theory focuses on size-selective survival through predation on the smaller individuals in a cohort (Chevalier 1973; Nielsen 1980).

In this study, size-selective mortality had already occurred during summer and autumn. Food (zooplankton, macrofauna) seems, however, insufficient to sustain the condition of non-piscivorous pikeperch. Pikeperch of 7 cm, weighing 2.2 g, were analysed both in August and September. Stomachs contained zooplankton and *Neomysis* and the absolute difference in energy content was $2.2 \times (19.8 \times 0.190 - 20.5 \times 0.196) = -0.616$ kJ. At routine metabolism, the oxygen consumption at 20°C is $0.3 \times (2.2)^{0.8}$ ml.h⁻¹ (Winberg 1961). For starving fish the energy loss over a 28 day period at 16.8°C would be 5.601 kJ. Consequently the energy loss of 7 cm pikeperch from August to September was 11% of the likely loss after a similar period of starvation. The observed energy contents and fat levels in 6 to 9 cm age 0 pikeperch point, however, towards a poor condition. Yellow perch of 13-18 cm which were starved until mortality occurred contained 2.1% fat based on dry weight (Newsome and Leduc 1975). Age 0 yellow in fed and starved treatments suffered 1 and 46% mortality, respectively, mortality being higher among the smaller individuals (Post and Evans 1989). The hypothesis whether planktivorous age 0 pikeperch die of starvation or whether the poor condition of the planktivores results in a higher vulnerability to other causes of mortality such as disease and predation cannot be addressed at this time. Starvation experiments should be conducted to verify whether the smallest specimens in a cohort are able to survive, given the presently observed energy contents per unit dry weight.

Strong year-classes are characterised by a mean length which is larger than average (Willemsen 1977). The new extended dataset confirms this by showing a positive correlation between length and survival of age 0 pikeperch. The lower energy content of small non-piscivorous pikeperch, their declining

importance in the length-frequency distribution, and the long-term observation that size and YCS are positively correlated, support the assumption that the onset of piscivory in pikeperch populations is an important, and perhaps the most important, YCS-determining process.

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REFERENCES

- Adams, S.M., and D.L. Angelis. 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. p. 103-117. *In* W.C. Kerfoot and A. Sih [ed.] Predation. Direct and indirect impact on aquatic communities. University Press of England, Hannover.
- Adams, S.M., R.B. McLean, and M.M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. *Can. J. Fish. Aquat. Sci.* 39: 1175-1184.
- Aggus, L.R., and G.V. Elliott. 1975. Effects of cover and food on year-class strength of largemouth bass. p. 317-322. *In* R.H. Stroud and H. Clepper [ed.] Black bass biology and management. Sport Fishing Institute, Washington D.C., USA.
- Brafield, A.E. 1985. Laboratory studies of energy budgets. p. 257-281. *In* P. Tytler and P. Calow [ed.] Fish energetics: new perspectives. Hopkins University Press, Baltimore, England.
- Brasseur, S.M.J.M. 1990. Interacties tussen bestanden aan jonge spiering, baars en snoekbaars en hun voedselorganismen in het IJsselmeer (Interactions between stocks of juvenile smelt, perch and pikeperch and their prey in Lake IJssel). Department of Fish Culture and Fisheries, Agricultural University Wageningen. MSc-thesis no. 1297. 92 p. + appendices (in Dutch with English summary)
- Buijse, A.D., L.A. Schaap, and T.P. Bult. 1992. The influence of water clarity on the catchability of six freshwater fish species in bottom trawls. *Can. J. Fish. Aquat. Sci.* 49: 000-000.
- Busch, W.-D.N., R.L. Scholl, and W.L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in Western Lake Erie, 1960-70. *J. Fish. Res. Board Can.* 32: 1733-1743.
- Chevalier, J.R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. *Trans. Am. Fish. Soc.* 102: 739-744.
- Chodorowski, A. 1975. Formation de populations bimodales chez les alevins de poissons carnassiers. *Verh. Internat. Verein. Limnol.* 19: 2546-2555.
- Clady, M.D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. *J. Fish. Res. Board Can.* 33: 1887-1893.

- DeAngelis, D.L., and C.C. Coutant. 1982. Genesis of bimodal size distributions in species cohorts. *Trans. Am. Fish. Soc.* 111: 384-388.
- Densen, W.L.T. van. 1985. Piscivory and the development of bimodality in the size distribution of 0+ pikeperch (*Stizostedion lucioperca* L.). *Z. angew. Ichthyol.* 3: 119-131.
- Densen, W.L.T. van, and J. Vijverberg. 1982. The relations between 0+ fish density, zooplankton size and the vulnerability of pikeperch, *Stizostedion lucioperca*, to angling in the Frisian lakes. *Hydrobiologia* 95: 321-336.
- Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *J. Fish. Res. Board Can.* 34: 1524-1550.
- Keast, A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Environ. Biol. Fish.* 12: 119-129.
- Keast, A., and J.McA. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. *Trans. Am. Fish. Soc.* 114: 204-213.
- Koonce, J.F., T.B. Bagenal, R.F. Carline, K.E.F. Hokanson, and M. Nagiec. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. *J. Fish. Res. Board Can.* 34: 1900-1909.
- LeCren, E.D. 1987. Perch (*Perca fluviatilis*) and pike (*Esox lucius*) in Windermere from 1940 to 1985: studies in population dynamics. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2): 216-228.
- McIntyre, D.B., F.J. Ward, and G.M. Swanson. 1987. Factors affecting cannibalism by pond-reared juvenile walleyes. *Prog. Fish-Cult.* 49: 264-269.
- Newsome, G.E., and G. Leduc. 1975. Seasonal changes in the yellow perch (*Perca flavescens*) of two Laurentian lakes. *J. Fish. Res. Board Can.* 32: 2214-2221.
- Nielsen, L.A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *J. Fish. Res. Board Can.* 37: 11-19.
- Oliver, J.D., G.F. Holeton, and K.E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Trans. Am. Fish. Soc.* 109: 611-616.
- Post, J.R., and D.O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Can. J. Fish. Aquat. Sci.* 46: 1958-1968.
- Shelton, W.L., W.D. Davies, T.A. King, and T.J. Timmons. 1979. Variation in growth of the initial year class of largemouth bass in West Point Reservoir, Alabama and Georgia. *Trans. Am. Fish. Soc.* 108: 142-149.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry*. Second Edition. W.H. Freeman and Company. New York. 859 p.
- Timmons, T.J., W.L. Shelton, and W.D. Davies. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama and Georgia. *Trans. Am. Fish. Soc.* 109: 176-186.
- Wicker, A.M., and W.E. Johnson. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. *Trans. Am. Fish. Soc.* 116: 264-271.

Willemsen, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34: 1710-1719.

Willemsen, J. 1983. Biology and management of pikeperch. Proc. 3rd Brit. Freshw. Fish. Conf., Univ of Liverpool. p. 115-125.

Winberg, G.G. 1961. Novye dannye ob intensivnosti obmena u ryb (New information on metabolic rate in fishes). Voprosy Ikhtiologii 1: 157-165. (Fish. Res. Board Can., Transl. Ser. No. 362.)

Chapter 5

FLEXIBILITY IN THE ONSET OF PISCIVORY AND GROWTH DEPENSATION IN EURASIAN PERCH, *PERCA FLUVIATILIS* L..

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ABSTRACT

Growth and size distributions of Eurasian perch (*Perca fluviatilis*) were studied in relation to prey choice and water temperature in Lake IJssel, The Netherlands. Growth of age 0 perch is density-dependent and positively influenced by high summer temperatures. Between 10 and 20 cm perch switched from a diet of zooplankton and macrofauna towards fish. Age 0 European smelt (*Osmerus eperlanus*) was the main fish prey. The onset of piscivory, defined as the length at which 50% of the perch with a full stomach contained fish, varied between 11.0 and 15.6 cm. The onset of piscivory occurred at a larger length when mean length of daphnids was high or when age 0 smelt densities were low. Growth was faster for piscivores than for non-piscivores. Consequently, size distributions of cohorts of which only the larger ones were piscivorous became positively skewed, and initial growth differences between males and females were enhanced. Besides on age 0 smelt, perch also fed on age 1 smelt, age 0 perch and age 0 ruffe (*Gymnocephalus cernua*), but Ivlev indices revealed a preference for age 0 smelt. Cannibalism by older age-groups was rare in 1987 and 1988, but became common in the northern part of the lake in 1989 when age 0 densities of perch were 30 times as high as in the two preceding years.

INTRODUCTION

Growth depensation, defined as the divergence in size over time among individuals within the same age-group (Keast and Eadie 1985) and induced by size-specific feeding patterns, is well known for obligatory piscivores like pikeperch, *Stizostedion lucioperca* (Buijse and Houthuijzen 1992; Chodorowska and Chodorowski 1975; Van Densen 1985b; Nagieć 1977; Schlumpberger 1962) and largemouth bass, *Micropterus salmoides* (Keast and Eadie 1985; Shelton et al. 1979; Timmons et al. 1980). Both species already in their first growing season exhibit a shift towards piscivory. The differential feeding pattern generally leads to bimodal size distributions, because the piscivores grow significantly faster than the plankton-eating or macrofauna-eating members of the same cohort (Van Densen 1985b; Shelton et al. 1979; Timmons et al. 1980). The onset of piscivory in these two species can be regarded as a crucial mechanism in year-class formation, because almost solely those age 0 fish which become piscivore will recruit to the adult population (Aggus and Elliott 1975; Buijse and Houthuijzen 1992; Van Densen 1985b; Wicker and Johnson 1987).

Variation in growth of Eurasian perch, *Perca fluviatilis*, and yellow perch (*Perca flavescens*) has been attributed to temperature (LeCren 1958; Neuman 1976), food type (Jeziarska 1974), and food density (Rask and Raitaniemi 1988). In natural situations, yellow perch normally become piscivorous at an older age than pike (*Esox lucius*) and largemouth bass (Keast 1985). The stunted growth of perch in some smaller water bodies in The Netherlands (Deelder 1951) and in Swedish lakes (Alm 1946) is ascribed to the low availability or absence of smelt. Differential growth within an age-group of perch induced by differential food availability has seldom been described. In fish ponds in southern France, cannibalism by the age 0 perch induced the formation of bimodal size distributions (Chodorowski 1975). In a Dutch lake with high densities of age 0 smelt (*Osmerus eperlanus*), which represents a potential prey, no piscivorous age 0 perch was observed (Van Densen 1985a).

In the present study we examined the consequences of temperature and feeding behaviour for the growth and size distributions of perch age-groups in Lake IJssel, The Netherlands. Earlier feeding studies in this lake had shown that up to a length of 5 cm zooplankton is the main food, supplemented by chironomid larvae (Willemsen 1977). The main transitional food organisms between zooplankton and fish are *Neomysis integer* and *Gammarus* spp., whereas fish predominate in the diet of perch over 10 cm. Growth depensation due to a switch to a piscivorous feeding mode might be expected in the second growing season when the fish reach a size of 10 cm. Therefore, the size structure per cohort was studied in relation to the onset of piscivory. Variability

in the onset of piscivory is likely to be governed by variations in type and density of alternative food items, and was compared with the availability of zooplankton and of prey fish. The short-lived smelt and ruffe (*Gymnocephalus cernua*) represent the major species of fish prey. Willemsen (1977) suggested that perch has a preference for smelt among the potential fish prey. Therefore, densities of prey fish were compared with their frequencies as food item in stomachs.

Since 1975, Lake IJssel is divided into two parts which have similar temperature regimes and fluctuations. Comparison of the growth and feeding behaviour of perch in the two parts was used to validate the hypothesis that diet influences the growth.

MATERIAL AND METHODS

Study area

Lake IJssel (52°45'N, 5°20'E), which has undergone profound changes due to land reclamation projects since it was closed from the sea in 1932, is a 182,000 ha shallow eutrophic lake, formerly an inland sea, divided into a northern basin (112,000 ha) and a southern basin (70,000 ha) by the construction of a dyke in 1975 (Fig. 1). The northern basin has an average depth of 4.5 m, with depressions up to 10 m deep caused by former tidal movements. The southern basin has an average depth of 3.6 m. Water clarity in both parts varies between 0.1 and 2 m Secchi disk depth, averaging 0.65 m. In both basins, the annual average water temperature is 10.4°C and varies annually from 0 to 25°C (Willemsen 1977). Over the period 1983-1986 total phosphorus levels averaged 0.28 mg.L⁻¹ and 0.15 mg.L⁻¹, and chlorophyll *a* 0.08 mg.L⁻¹ and 0.05 mg.L⁻¹ in the northern and southern part, respectively.

The most common fish species are eel (*Anguilla anguilla*), smelt, the cyprinids bream (*Abramis brama*) and roach (*Rutilus rutilus*) and the percids perch, pikeperch and ruffe. The smelt stock is composed of a short-lived land-locked population together with a much smaller migratory population. The land-locked component attains a length of circa 7 cm after one year and 10 cm after two years. There is a commercial fishery for pikeperch and perch with gill nets (101 mm stretched mesh), for eel with fyke nets, eel boxes and long lines, and for spawning smelt with fyke nets (Van Densen et al. 1990). The gill net fishery is opened from July 1 until March 15, but is practised mainly in autumn and winter. Minimum legal size of perch is 22 cm, but in the gill nets only fish from 25 cm onwards are caught. Average annual instantaneous fishing mortalities, based on cohort analysis, were 0.02, 0.34, 0.93, 1.20 and 0.88 for

age 2 to 6 fish of the year-classes 1969 to 1981 in the period from 1970 to 1987 (Buijse et al. 000).

Fish sampling

Fish were sampled in Lake IJssel in the period 1987 - 1989 with two types of bottom trawls at 22 sampling sites (Fig. 1). Every year three surveys were carried out during the summer period and one in autumn:

1987: 29 June - 3 July, 17-21 August, 7-10 September and 9-12, 17 November

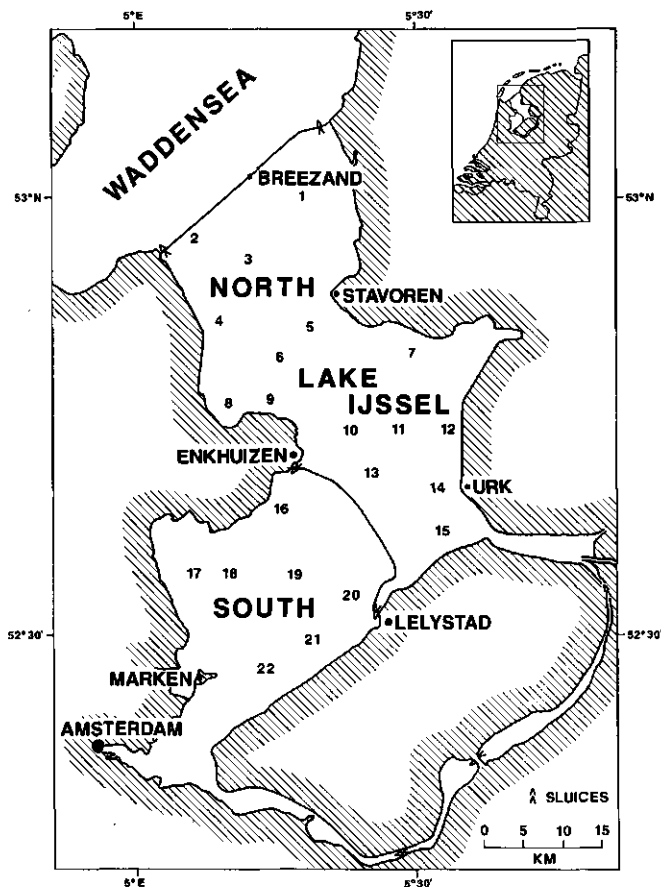


Fig. 1. Location of Lake IJssel and of the sampling sites (1 to 22) used during the trawl surveys. Water temperatures were measured daily at Marken, Enkhuiizen, Urk, Stavoren and Breezand.

- 1988: 27-30 June, 15-18, 22-23 August, 12-16 September and 14-17, 23 November
1989: 19-22 June, 14-17, 21-22 August, 11-15 September and 13-16, 20 November

Trawling in June-July was carried out with a 2-mm stretched mesh bottom trawl (upper-rope 6.75 m; bottom rope 7.25 m, danleno height 0.75 m) and in August, September and November with a 20-mm stretched mesh bottom trawl (upper-rope 13 m; bottom rope 14.75 m; danleno height 1 m). The trawls were kept open with a 8-m beam and two danlenos. The towing speed was 1.1 m.s^{-1} in 1987 and 1989 and 1.4 m.s^{-1} in 1988 with the 2-mm trawl and 1.6 m.s^{-1} in every year with the 20-mm trawl. Haul duration was 10 min.

The fish were sorted by species on deck, weighed to the nearest 0.1 kg, and individual fish were measured to the nearest cm total length. During surveys in June age 0 fish were preserved in 4% formalin for later identification and length measurement in the laboratory.

Indices of abundance were based on the geometric means of the catches (adding 1) in individual hauls for the northern and southern part separately. All catches were first standardised to 1000 m trawling, which is about the distance covered in 10 minutes with the 20-mm bottom trawl. Since the width of the 2-mm trawl is about half the width of the 20-mm trawl, catches originating from the 2-mm trawl were doubled to be comparable with catches made by the 20-mm trawl. No adjustments have been made for possible differences in catchability between those trawls.

Length frequency (LF) data on perch were available from former 20-mm bottom trawl surveys from 1966 to 1986 and have been used for estimation of mean length at age of age 0 and 1 fish and year-class strength. Year-classes are henceforward indicated in the text with square brackets.

Age determination and stomach analysis

Age distributions per size-class for age 1 and older perch were estimated by reading opercula according to LeCren (1947). In case opercula were taken for age determinations, total length of perch was measured to the nearest mm.

Sex, maturity and stomach contents per cm-class were examined macroscopically. The food categories were scored as frequency of occurrence (FOO). Fish prey were identified per species and age-group. The number of stomachs per cm-class that contained unrecognizable fish remainders were proportionally split, assuming that all fish prey were digested at the same rate. In addition, age 0 and age 1 perch were also taken to the laboratory for microscopic determination of the species and size composition of the zooplankton in their stomachs.

Sampling of zooplankton

To study species and size composition of zooplankton, water samples were taken at two depths (1 m below the water surface and 1 m above the bottom) at every sampling site during the surveys from June to September. The samples per site were combined and sieved through a 120 μm filter. In 1987 a 5-L Friedinger sampler, and in 1988 and 1989 an 11.8-L Schindler-Patalas sampler was used. Samples were preserved using 4% formalin. Zooplankton samples were taken to the laboratory for quantitative microscopic determination of the species and size composition. No data were collected to estimate abundances of chironomids, *Gammarus* spp. and *Neomysis integer*.

Data treatment

The LF-distributions of prey fish in the trawl catches were split into age-groups for comparison with the age distribution in the stomachs. Age 0 perch and roach were always discrete in the LF- distribution; age 0 smelt and ruffe only during the first survey in June. If consecutive cohorts of smelt or ruffe overlapped in the distribution, the cohort strength of the age 0 fish (N_0) was estimated by:

$$N_0 = \sum_{i=1}^{n-1} C_i + C_n * \frac{m_0 * d_1^2}{m_0 * d_1^2 + m_1 * d_0^2} \quad (1)$$

where:

- C = the number of fish in size-class i or n
- i = size-class
- n = the size class with the lowest number, which is situated between two modi
- m_0 = the number of fish in the modal size-class of age 0
- m_1 = the number of fish in the modal size-class of age 1
- d_0 = distance in size-classes between the size-class of the modus of age 0 and size-class n
- d_1 = distance in size-classes between the size-class of the modus of age 1 and size-class n

The stocks of smelt and ruffe mainly consist of two age-groups only. Age 2 and older could not clearly be identified within the frequency distributions. Therefore the number of age 1 fish was obtained by subtracting the number of age 0 fish from the total.

Table 1. Water temperature (dd14 = the total yearly sum of degree days over 14°C), abundance of age 0 perch (N_0 = geometric mean number.(10 min trawling)⁻¹) and mean length of age 0 and age 1 perch (TL = cm total length) in the northern and southern part of Lake IJssel over the period 1966-1989.

| year | dd14 | northern part | | | southern part | | |
|------|------|----------------|-------------|-------------|----------------|-------------|-------------|
| | | age 0 N_0 | age 0 TL | age 1 TL | age 0 N_0 | age 0 TL | age 1 TL |
| 1966 | 428 | 6 | 7.8 | | 2 | 7.5 | |
| 1967 | 481 | 3 | 7.7 | | 0 | 8.5 | 16.3 |
| 1968 | 432 | 3 | 7.4 | | 3 | 7.9 | |
| 1969 | 550 | 98 | 8.7 | | 255 | 8.4 | 18.9 |
| 1970 | 473 | 169 | 6.8 | 17.2 | 251 | 6.8 | 16.9 |
| 1971 | 477 | 155 | 7.1 | 14.3 | 84 | 7.8 | 15.2 |
| 1972 | 361 | 3 | 7.3 | 12.5 | 2 | 7.0 | 13.2 |
| 1973 | 527 | 136 | 7.8 | | 22 | 8.5 | |
| 1974 | 386 | 0 | 8.2 | 13.6 | 32 | 7.7 | 14.7 |
| 1975 | 555 | 621 | 7.9 | | 393 | 8.8 | 16.2 |
| 1976 | 567 | 221 | 7.5 | 15.4 | 146 | 8.5 | 16.7 |
| 1977 | 346 | 4 | 7.4 | 12.3 | 42 | 6.9 | 12.8 |
| 1978 | 325 | 74 | 7.7 | | 1286 | 7.2 | 13.7 |
| 1979 | 372 | 29 | 6.8 | 13.6 | 8 | 6.8 | 11.4 |
| 1980 | 405 | 122 | 7.4 | 13.8 | 96 | 7.4 | |
| 1981 | 443 | 4 | 8.5 | 14.3 | 6 | 9.1 | 13.7 |
| 1982 | 571 | 40 | 9.2 | | 354 | 8.2 | |
| 1983 | 521 | 115 | 8.1 | 17.7 | 187 | 7.4 | 13.7 |
| 1984 | 361 | 26 | 8.1 | 14.4 | 33 | 8.0 | 13.4 |
| 1985 | 379 | 775 | 6.9 | 16.2 | 71 | 7.0 | 12.0 |
| 1986 | 438 | 301 | 7.1 | 12.1 | 385 | 6.8 | 12.5 |
| 1987 | 409 | 16 | 7.1 | 12.6 | 18 | 6.9 | 12.0 |
| 1988 | 378 | 17 | 6.9 | | 5 | 7.0 | |
| 1989 | 615 | 207 | 7.8 | | 41 | 8.5 | |
| mean | 450 | 131 | 7.6 | 14.3 | 155 | 7.7 | 14.3 |

The percentage of piscivores per cm-class is described with a logistic function with the midpoint being the length at which 50% of the full stomachs contained fish. This midpoint (L_{50}) is used as an index for the onset of piscivory and was estimated by linear regression using data from 10 to 20 cm perch for which a minimum of 10 stomachs had been examined (Appendix 1).

$$\ln\left(\frac{F_L}{100-F_L}\right) = a(L-L_{50}) \quad (2)$$

where:

- F_L = observed frequency of occurrence of fish in full stomachs of perch with length L (%)
- a = constant
- L = length (cm)
- L_{50} = length at which 50% of the full stomachs contained fish (cm)

Water temperature

Daily water temperatures over the entire season were available from samples taken at five sites at 9:00 MET (Fig. 1).

RESULTS

Growth

In Lake IJssel for age 0 to 5 fish mean lengths at age were 8, 15, 21, 26, 29, 31 cm, and females grow slightly faster than males (Willemsen 1977). Mean length of age 0 fish varied between 1966 and 1989 from 6.8 to 9.2 cm, and for age 1 from 11.4 to 18.9 cm (Table 1, Fig. 2). Mean length at age 0 in the northern and southern part, and mean length at age 1 in the southern part correlated significantly with water temperature, expressed as the sum of degree days over 14°C (DD14). As an example, LF-distributions of age 0 and age 1 of year-classes [82] and [85] in the northern part show the large variation in growth (Fig. 2). Mean lengths of [82] and [85] were respectively at 9.2 and 6.9 cm after one year and diverged to 17.7 and 12.1 cm after two years. Year-class [82] experienced much higher water temperatures in 1982 and 1983 (DD14 = 571 and 521 °C.d) than [85] in 1985 and 1986 (DD14 = 379 and 438 °C.d). Besides temperatures also densities of age 0 perch influenced growth of age 0 as can be seen from the following equation:

$$TL = 0.00552 \cdot DD14 - 0.110 \cdot \log_e N_0 + 5.58$$

$n = 48, r^2 = 0.41, p < 0.001.$

where:

- TL = mean length of age 0 perch in November (nearest cm total length)
DD14 = total annual sum of degree days over 14°C (d.°C)
N₀ = geometric mean number of age 0 perch per standard trawl haul in November (number.(10 min trawling)⁻¹)

E.g. [82] was nine-fold stronger in the southern part than in the northern part, resulting in a retarded growth in the southern part with modes at 8.2 and 13.7 cm for age 0 and 1 respectively.

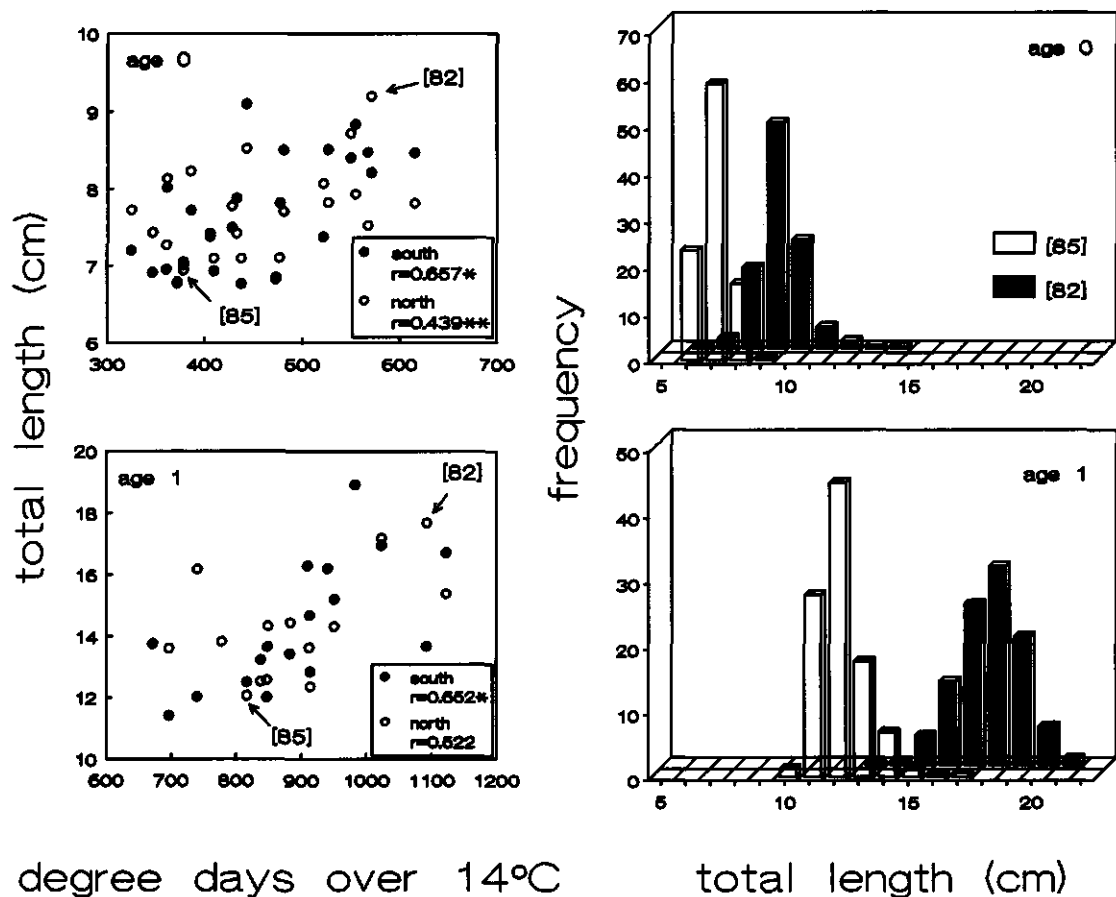


Fig. 2. Mean length of age 0 and age 1 perch versus the total sum of degree days over 14°C in the first year and in the first two years respectively (data for 1966-1989; some weak year-classes were omitted, because they could not be distinguished in the length frequency distributions). For the slowly growing year-class [85] and the fast growing year-class [82] in the northern part of Lake IJssel length frequency distributions of age 0 and age 1 are displayed. r = correlation coefficient; * $p < 0.05$; ** $p < 0.01$; number of observations (n): $n=24$ for age 0 fish in both parts; $n=14$ and $n=17$ for age 1 fish in the northern and southern part respectively.

Food

The most important food items in the stomachs of perch were zooplankton (mainly *Daphnia* spp., cyclopoid copepods, *Bosmina coregoni*, *Alona affinis* and *Leptodora kindtii*), chironomid pupae and larvae, macrofauna (*Gammarus* spp. and *Neomysis integer*), and fish. Fish categories found most often were age 0 smelt, ruffe and perch and age 1 smelt, while bullhead (*Cottus gobio*), eel and age 0 pikeperch, roach and bream, and age 1 perch and ruffe were found occasionally. The results of 10,388 examined stomachs of perch are listed per size-class in Appendix 1. Based on this generalised description of the onset of piscivory and the mean yearly LF-distributions of the perch stock in the northern and southern part from 1966 to 1989, 80% of the perch stock biomass ($n=46$, $SD=15\%$, $min=28\%$, $max=96\%$) on average would have been piscivorous.

Perch always switched between 10 and 20 cm from eating zooplankton, *Gammarus* and *Neomysis* towards eating fish (Fig. 3). The length at onset of piscivory varied circa 4.5 cm, from 11.0 cm in the southern part in September 1988 to 15.6 cm in the northern part in June 1987, and varied more between years and lake parts than between sampling periods in a lake part in a certain year. Thus the onset of piscivory was at a greater length, and zooplankton was a more important food item in the northern part in 1987 than in all other situations. In the southern part macrofauna was always more important than zooplankton for perch over 10 cm. *Neomysis* was occasionally an important food item, e.g. in the southern part in August and September 1987.

In Lake IJssel, onset of piscivory means onset of eating age 0 smelt (Fig. 4). Age 1 smelt became more frequent in stomachs of larger perch, and became as frequent as age 0 smelt only in stomachs of perch larger than 26 cm, which clearly indicates size-selective predation. Age 1 smelt was found in perch of 13 cm and larger. The same holds for age 0 perch and ruffe, but they were occasionally found in smaller perch. In 1987 and 1988 age 0 perch rarely were found in stomachs, but in 1989 it was the second most important food item for piscivorous perch in the northern part. Similarly, ruffe was the second most important food item over a wide range of predator sizes in the southern part in 1989. Like age 1 smelt and age 0 ruffe the importance of age 0 perch increased with increasing predator size. These data show that the food spectrum of perch is very flexible, since shifts took place over a wide range of predator sizes and varied considerably among place and time.

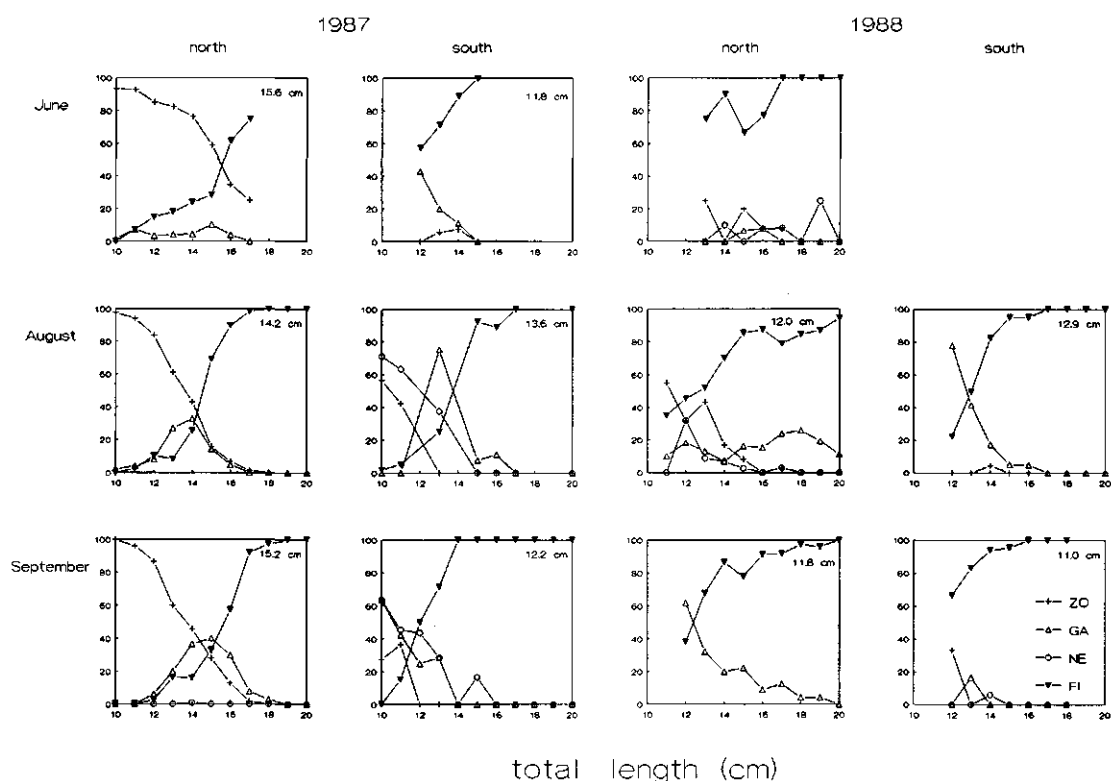


Fig. 3.

Frequencies of occurrence of zooplankton (ZO), *Gammarus* spp. (GA), *Neomysis integer* (NE) and fish (FI), expressed as percentages of fish with full stomachs, in 10 to 20 cm perch in the northern and southern part of Lake IJssel in June, August and September 1987 and 1988. The sum of the frequencies of different food items can surpass 100%, since stomachs regularly contained more than one food item. The estimated length by which 50% of the full stomachs contained fish is given in the upper right hand corner (no reliable estimate could be made for the northern part in June 1988). Only those cm-classes per sampling period are presented, which had 10 or more examined stomachs (Appendix 1).

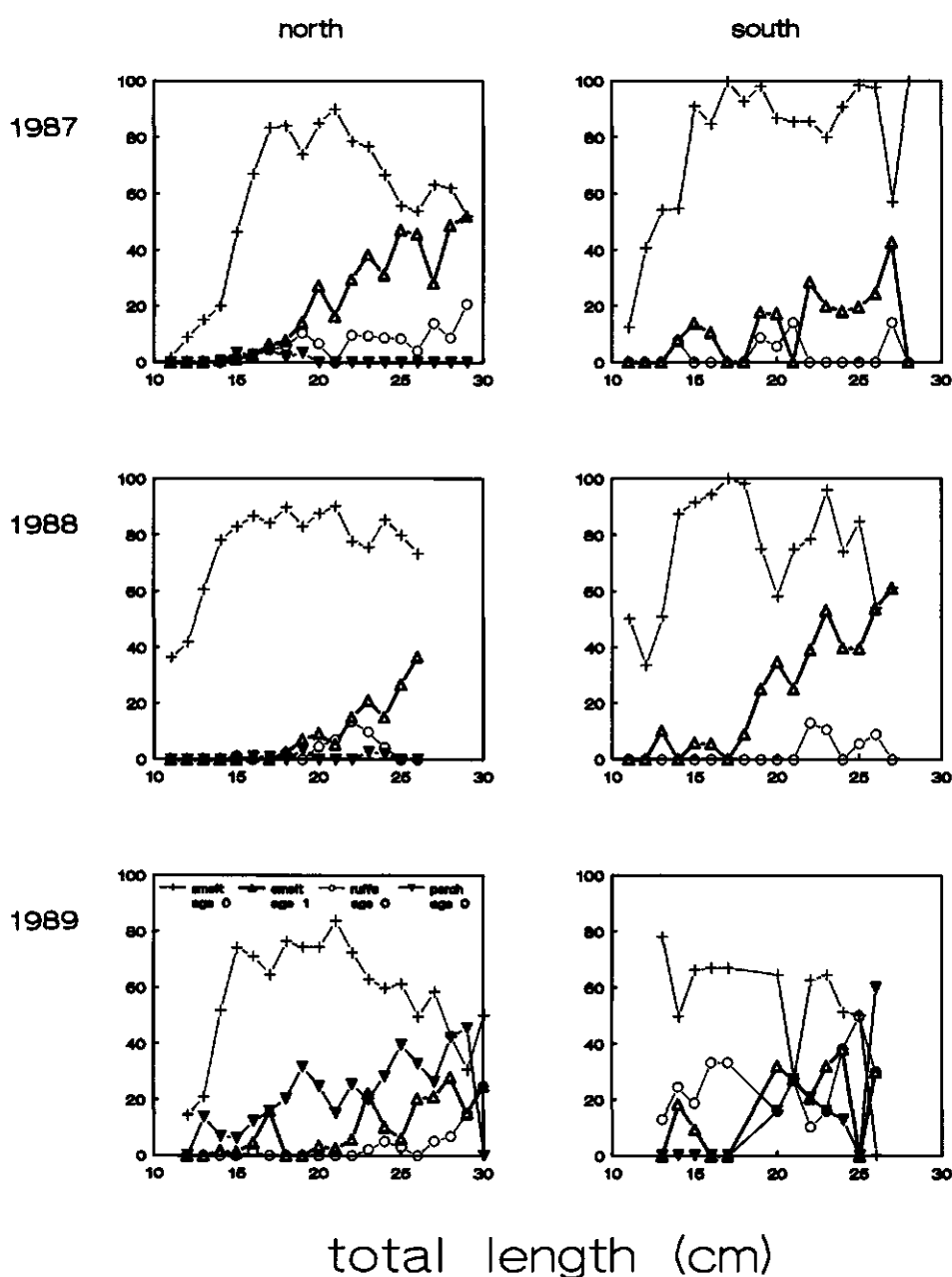


Fig. 4. Frequencies of occurrence of age 0 smelt, age 1 smelt, age 0 ruffe and age 0 perch, expressed as percentages of fish with full stomachs, in 10 to 30 cm perch in the northern and southern part of Lake IJssel in 1987 to 1989. August and September data are summarised per year and part of the lake.

Growth depensation within cohorts

The enhancement of growth of perch by eating fish is explained in this section by comparing growth of perch from both lake parts or growth of various age-groups in the same year. The growth and size distributions of perch belonging to year-classes [85] - [88] have been studied in detail. Data from [85] in the northern part will be used to illustrate growth depensation as a consequence of the onset of piscivory. Data from [85] in the southern part, and the [86] - [88] will be used to supply circumstantial evidence. The effect of the onset of piscivory on the size composition was investigated by calculating the skewness and the coefficient of variation (VC), which are assumed to increase when growth depensation occurs.

In the northern part both [85] and [86] were strong year-classes in terms of numbers of age 0 perch caught per haul during autumn trawl surveys, while [87] and [88] were weak (Table 1). Growth of age 0 and 1 perch of both [85] and [86] was less than average. Growth depensation was clearly manifested for [85]: the LF-distribution of age 0 and 1 fish was only slightly skewed, but as age 2 (1987) it became positively skewed and the VC increased. Size ranges in the northern part were 6 - 9 cm in November 1985, 9 - 16 cm in November 1986, 13 - 22 cm in September 1987 and 15 - 26 cm in September 1988 for sexes combined (Fig. 5). Depensation was less for [86] as reflected by a lower VC. Size distributions are displayed only up till September 1988, because at that time [85] became vulnerable for the size-selective impact of the gill net fishery, catching perch from 25 cm onwards. In the southern part growth depensation of [85] was slightly less than in the northern part, and size distributions were less skewed (Fig. 6). Here size ranges were 5 - 10 cm in November 1985, 9 - 15 cm in November 1986, 13 - 21 cm in September 1987 and 19 - 28 cm in September 1988 for sexes combined.

The increase in skewness coincided with the onset of piscivory, which is indicated by an arrow. In 1987 onset of piscivory took place for age 2 perch in both parts of the lake. The size at the onset of piscivory in 1987 implied that at first only the larger individuals of age 2 perch were piscivorous, and that the fraction of age 2 fish that were piscivorous increased from June to September. In the southern part in September age 2 fish had fully become piscivorous, as did a part of age 1 fish. In the northern part a smaller fraction of age 2 fish was piscivorous than in the southern part. In 1988 the onset of piscivory took place in both parts for age 1 perch, which resulted in a faster growth than that of age 1 fish in the two preceding years. This year-class [87] was too weak to supply information on changes in the shape of size distributions.

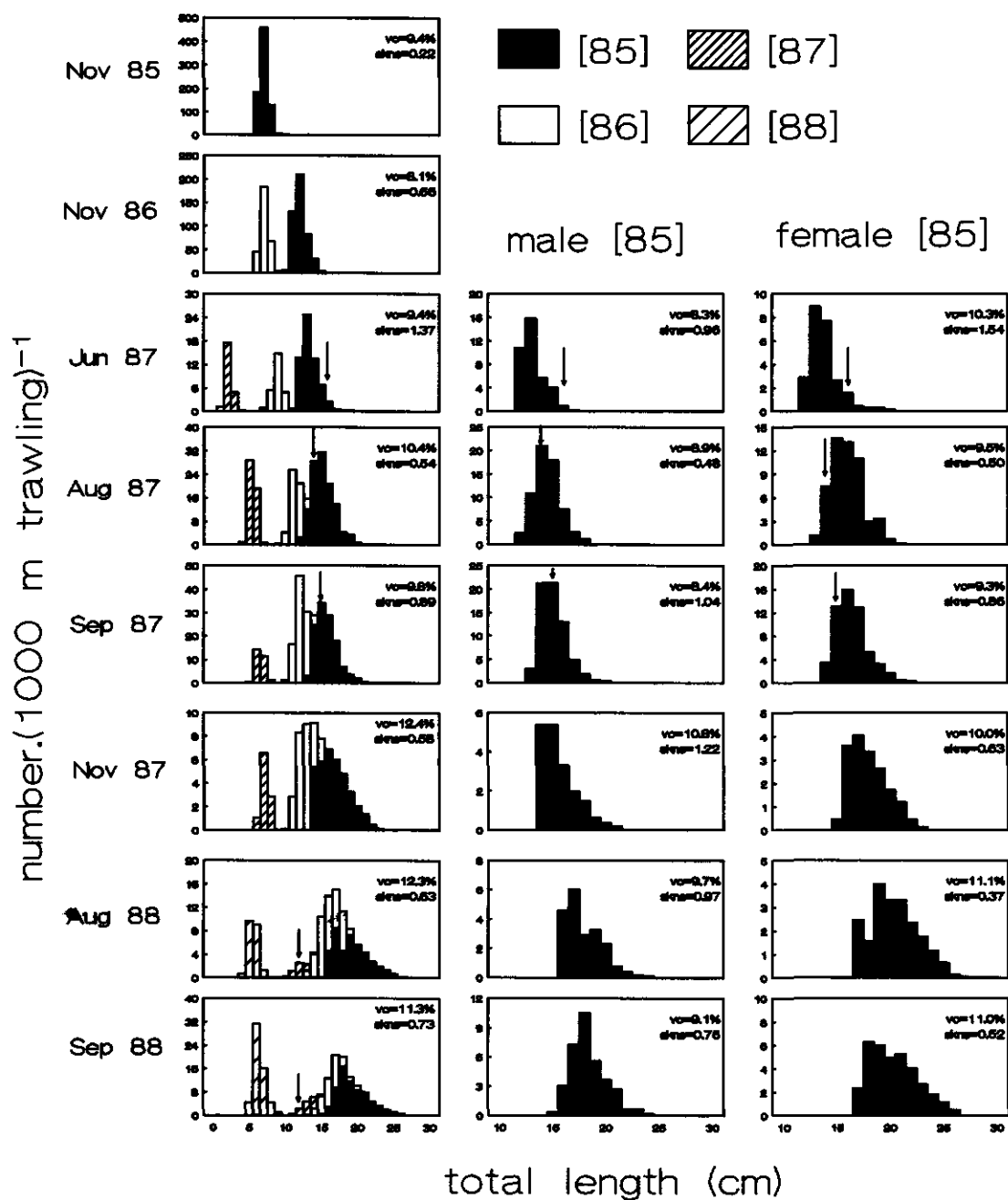


Fig. 5. Length frequencies of the year-classes [85] - [88] of perch in the northern part of Lake IJssel from 1985 to 1988. In 1987 and 1988 [85] is split into sexes. Arrows indicate the size-class at which 50% of the full stomachs contained fish. VC is the coefficient of variation and SKNS is the skewness of year-class [85]. Give notice to the variable Y-axis scaling.

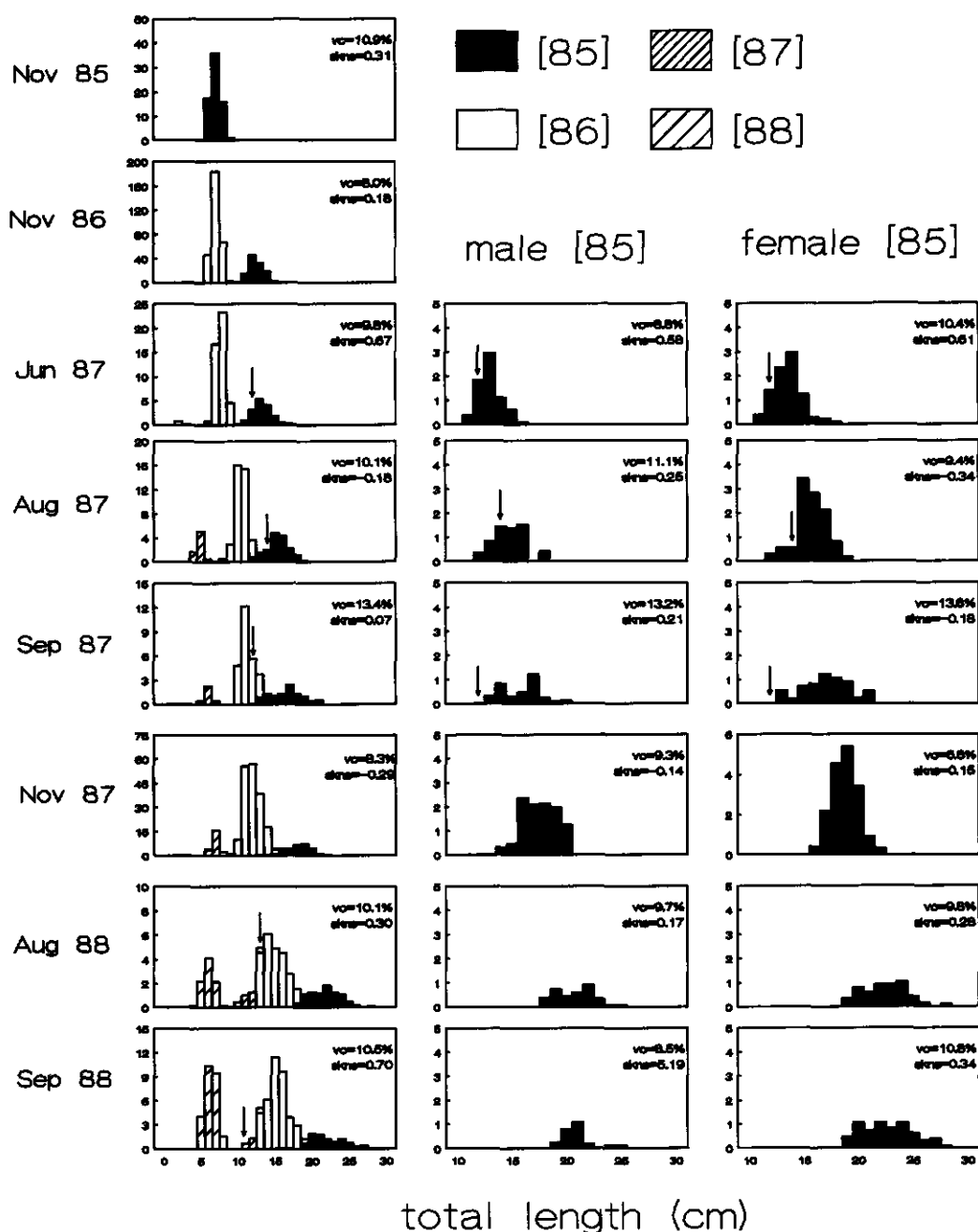


Fig. 6.

Length frequencies of the year-classes [85] - [88] of perch in the southern part of Lake IJssel from 1985 to 1988. In 1987 and 1988 [85] is split into sexes. Arrows indicate the size-class at which 50% of the full stomachs contained fish. VC is the coefficient of variation and SKNS is the skewness of year-class [85]. Give notice to the variable Y-axis scaling. The high skewness for males in September 1988 is mainly due to low numbers caught.

An increase in the skewness in the size distributions could have been the consequence of sex-related differences in growth rate: age 1 and older females always were larger than males, except for [87] in the northern part. Size distributions of males and females of [85] were both positively skewed. In the southern part this skewness was much less pronounced, possibly because there a greater part of the cohort had already become piscivorous. This earlier switch towards piscivory is illustrated by age 2 fish [85] in 1987, which showed a faster growth in the southern part than in the northern part. For all other year-classes growth was slower in the southern than in the northern part (Table 2).

Initial differences in length between males and females increased if the onset of piscivory took place within a cohort. From June to September 1987 the differences in length between age 2 males and females of [85] increased from 0.6 cm to 1.3 cm in the northern and to 1.2 cm in the southern part. The arrow indicates that more age 2 females than males had become piscivorous. Depensation was less for a cohort which fully recruited to a piscivorous feeding mode at the beginning of a new growing season preying upon a new cohort of smelt. E.g. year-class [86] was still almost non-piscivorous in 1987 but fully piscivorous in 1988, and the difference between male and female length did not increase. The initial difference at age 1 was 0.3 and 0.6 cm in the northern and southern part in September 1987 respectively, and at age 2 it was still only 0.4 cm in both parts of the lake in September 1988.

Simultaneous comparison of non-piscivorous younger age-groups with piscivorous older age-groups also showed that eating fish enhanced growth. According to the von Bertalanffy growth function growth in length of smaller and younger individuals is faster than that of larger and older fish, but the length increase of age 2 was larger than of age 1 and 0 fish in the northern part (Sep-Nov 1987) and in the southern part (Aug-Nov 1987). These growth differences were thought to be caused by food availability, because zooplankton concentrations were low during late summer and autumn, while prey fish was readily available.

Factors influencing the onset of piscivory

Size- and species-selective predation of perch has been demonstrated especially on daphnids (van Densen 1985a; Klemetsen 1973; Köpke et al. 1988; Mills et al. 1989), but also on cyclopoid copepods (Fentener van Vlissingen 1988; Houthuijzen 1989). Mean lengths of zooplankton can be used as an index for the exploitation rate by planktivores (Mills et al. 1987). The zooplankton in the lake consisted mainly of the cladocerans *Daphnia galeata*, *D. cucullata*, *Bosmina coregoni*, *B. longirostris*, *Chydorus sphaericus* and *Leptodora kindtii*, and cyclopoid copepods. The composition of the zooplankton in the lake was

Table 2. Mean length (cm total length) and coefficient of variation of the length (% in parentheses) of male and female perch of year-class [85] to [88] in the northern and southern part of Lake Issel. Males and females were identified for age 1 and older from June 1987 onwards.

| a. northern part | | | | | | | | | |
|------------------|-------------|-------------|-------------|-------------|------------|-------------|-------------------|-------------|-------------|
| month | [85] σ+σ | [85] σ | [85] ♀ | [86] σ+σ | [86] σ | [86] ♀ | [87] σ+σ | [87] σ | [88] σ+σ |
| Nov-85 | 6.9 (9.4) | | | | | | | | |
| Nov-86 | 12.0 (8.1) | | | 7.1 (9.1) | 8.9 (9.6) | 9.1 (8.1) | 2.2 (23.3) | | |
| Jul-87 | 13.4 (9.4) | 13.2 (8.3) | 13.8 (10.3) | 9.0 (8.9) | 11.2 (5.9) | 11.6 (7.1) | 5.4 (10.7) | | |
| Aug-87 | 15.2 (10.4) | 14.5 (8.9) | 16.0 (9.5) | 11.4 (6.8) | 12.0 (6.3) | 12.3 (7.1) | 6.5 (9.5) | | |
| Sep-87 | 15.7 (9.8) | 15.1 (8.4) | 16.4 (9.3) | 12.2 (6.7) | 12.4 (7.3) | 13.1 (9.3) | 7.2 (8.8) | | |
| Nov-87 | 16.8 (12.4) | 15.7 (10.8) | 18.0 (10.0) | 12.7 (8.7) | 15.5 (8.5) | 16.7 (8.6) | 12.0 (7.9) | 12.1 (9.8) | 5.5 (12.9) |
| Aug-88 | 19.2 (12.3) | 17.9 (9.7) | 20.4 (11.1) | 16.1 (9.3) | | | 13.1 (7.2) | 13.2 (6.2) | 6.4 (12.7) |
| Sep-88 | 19.4 (11.3) | 18.4 (9.1) | 20.3 (11.0) | 16.5 (8.8) | 16.3 (8.7) | 16.7 (9.1) | | | |
| b. southern part | | | | | | | | | |
| month | [85] σ+σ | [85] σ | [85] ♀ | [86] σ+σ | [86] σ | [86] ♀ | [87] σ+σ | [87] σ | [88] σ+σ |
| Nov-85 | 7.0 (10.9) | | | | | | | | |
| Nov-86 | 12.5 (8.0) | | | 6.8 (10.0) | 7.7 (9.5) | 7.7 (9.6) | 2.2 ¹⁾ | | |
| Jul-87 | 13.3 (9.8) | 13.0 (8.8) | 13.6 (10.4) | 7.7 (9.4) | 10.5 (7.4) | 10.6 (7.5) | 4.8 (11.3) | | |
| Aug-87 | 15.4 (10.1) | 14.7 (11.1) | 15.7 (9.4) | 10.5 (7.4) | 11.0 (6.9) | 11.6 (9.4) | 6.0 (10.0) | | |
| Sep-87 | 16.7 (13.4) | 15.9 (13.2) | 17.1 (13.8) | 11.3 (8.5) | 11.8 (9.3) | 12.3 (9.9) | 7.0 (9.6) | | |
| Nov-87 | 18.3 (8.3) | 17.5 (9.3) | 18.8 (6.7) | 12.1 (9.8) | 14.6 (9.2) | 15.3 (10.4) | 11.5 (9.2) | 11.3 (11.8) | 6.0 (14.0) |
| Aug-88 | 21.7 (10.1) | 20.7 (9.7) | 22.4 (9.8) | 14.9 (9.9) | | | | 12.3 (8.6) | 6.3 (13.1) |
| Sep-88 | 22.1 (10.5) | 20.9 (8.5) | 22.6 (10.8) | 15.3 (9.4) | 15.2 (9.7) | 15.6 (9.1) | 12.0 (7.6) | | |

¹⁾ numbers caught were too low to estimate the coefficient of variation.

characterised by mean lengths of the zooplankton groups, which were identified as important food items (*Daphnia* spp., cyclopoid copepods and *B. coregoni*) (Table 3). Mean size of daphnids was small in every situation except in the northern part in 1987. Daphnid length was larger in the northern part than in the southern part within the same sampling period. Mean lengths of the three zooplankton groups were smallest in 1988 except for cyclopoids in the southern part. No consistent differences for cyclopoid copepods and *B. coregoni* between both lake parts were found.

Table 3. Characteristics of important food items for perch in the northern and southern part of Lake IJssel from 1987 to 1989. Mean length of *Daphnia* spp., cyclopoid copepods and *Bosmina coregoni*., and abundance and mean length of age 0 smelt, age 1 smelt, age 0 ruffe and age 0 perch. Zooplankton was not sampled in November.

| Mean length of zooplankton (mm) | | 1987 | | 1988 | | 1989 | |
|---------------------------------|-----------|-------|-------|-------|-------|-------|-------|
| | | north | south | north | south | north | south |
| <i>Daphnia</i> spp. | June | 0.92 | 0.69 | 0.66 | 0.56 | 0.85 | 0.78 |
| | August | 0.82 | 0.67 | 0.69 | 0.62 | 0.79 | 0.74 |
| | September | 0.90 | 0.64 | 0.74 | 0.60 | 0.71 | 0.72 |
| cyclopoid copepods | June | 0.71 | 0.58 | 0.61 | 0.61 | 0.72 | 0.63 |
| | August | 0.66 | 0.49 | 0.63 | 0.65 | 0.76 | 0.69 |
| | September | 0.78 | 0.61 | 0.62 | 0.57 | 0.65 | 0.67 |
| <i>Bosmina coregoni</i> | June | 0.41 | 0.38 | 0.36 | 0.38 | 0.42 | 0.41 |
| | August | 0.43 | 0.39 | 0.37 | 0.35 | 0.40 | 0.40 |
| | September | 0.45 | 0.37 | 0.37 | 0.36 | 0.37 | 0.39 |

| Abundance (number.(1000 m trawling) ⁻¹) and, between brackets, mean total length (cm) | | 1987 | | 1988 | | 1989 | |
|---|-----------|------------|------------|------------|------------|------------|------------|
| | | north | south | north | south | north | south |
| age 0 smelt | June | 605 (3.6) | 3235 (3.4) | 4015 (3.9) | 6351 (3.8) | 1145 (3.6) | 2771 (3.8) |
| | August | 594 (6.2) | 1236 (5.6) | 1713 (5.7) | 1579 (5.3) | 421 (6.8) | 969 (6.3) |
| | September | 268 (6.8) | 1219 (6.1) | 1545 (6.0) | 1349 (5.7) | 424 (7.6) | 986 (6.8) |
| | November | 63 (7.7) | 3742 (6.5) | 1832 (6.5) | 1987 (6.0) | 384 (8.1) | 656 (7.5) |
| age 1 smelt | June | 169 (9.1) | 817 (7.9) | 103 (9.7) | 511 (8.3) | 154 (8.0) | 485 (7.7) |
| | August | 125 (9.9) | 260 (8.1) | 216 (10.2) | 1058 (8.2) | 248 (9.9) | 855 (8.0) |
| | September | 181 (10.1) | 513 (8.1) | 167 (9.9) | 992 (8.3) | 184 (10.4) | 588 (8.3) |
| | November | 18 (10.5) | 1520 (8.2) | 26 (10.6) | 64 (8.5) | 49 (10.9) | 170 (9.2) |
| age 0 ruffe | June | 218 (1.8) | 753 (1.3) | 8 (1.9) | 15 (1.4) | 899 (2.3) | 385 (1.7) |
| | August | 22 (5.2) | 72 (4.4) | 39 (5.6) | 683 (5.1) | 312 (6.5) | 206 (5.5) |
| | September | 195 (6.3) | 76 (5.3) | 375 (6.7) | 868 (5.8) | 261 (7.8) | 136 (6.2) |
| | November | 18 (7.5) | 1078 (6.3) | 37 (7.5) | 25 (6.4) | 31 (8.8) | 225 (7.1) |
| age 0 perch | June | 24 (2.2) | 1 (2.2) | 21 (2.5) | 2 (3.1) | 415 (2.4) | 9 (3.0) |
| | August | 50 (5.4) | 7 (4.8) | 21 (5.5) | 9 (6.0) | 1266 (6.7) | 133 (7.0) |
| | September | 27 (6.5) | 3 (6.0) | 58 (6.4) | 25 (6.3) | 1416 (7.4) | 64 (7.6) |
| | November | 11 (7.2) | 23 (7.0) | 13 (7.1) | 4 (7.1) | 459 (7.8) | 50 (8.3) |

Densities of age 0 smelt were highest in both parts of the lake in 1988 (Table 3). Mean length of age 0 smelt differed very little between the lakes during surveys in June 1987-89, but length attained in September ranged between 5.7 cm in the southern part in 1988 and 7.6 cm in the northern part in 1989, and always was larger in the northern part.

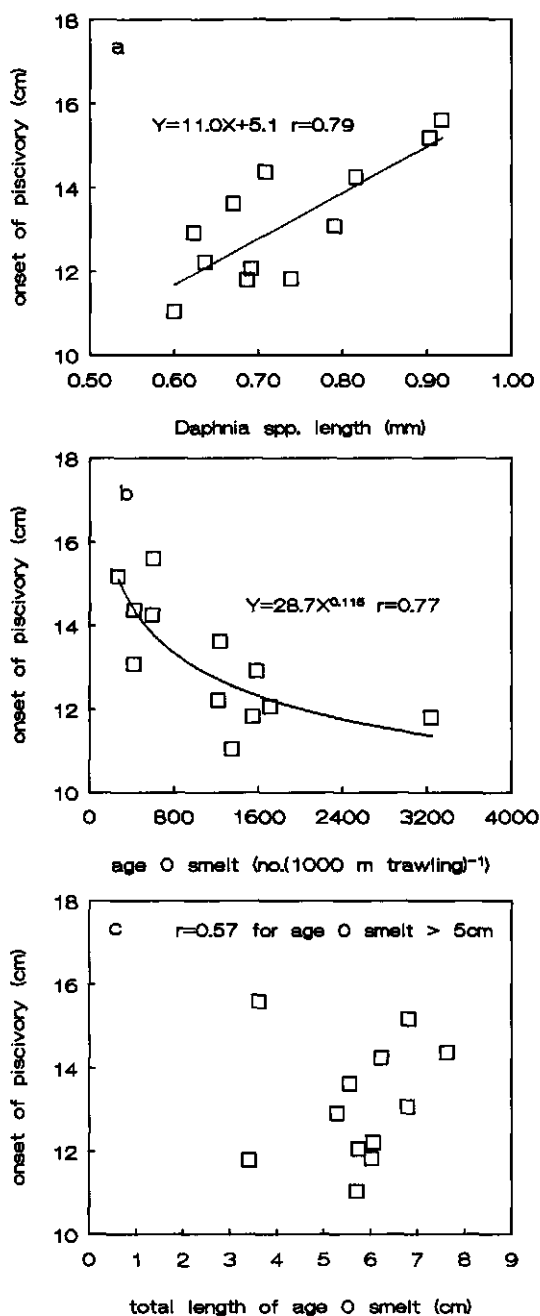


Fig. 7.

The onset of piscivory in perch, in terms of length at which 50% of the full stomachs contained fish, in relation to (a) the mean length of *Daphnia* spp., (b) the abundance of age 0 smelt, and (c) the mean length of age 0 smelt. For 12 out of 18 subsets (2 lake parts * 3 periods * 3 years) a reliable estimate of the 50% point could be made: June, August and September 1987, August and September 1988 from as well the northern as the southern part and August and September 1989 from the northern part.

Onset of piscivory, which showed large flexibility, was positively related to daphnid length, and inversely related to age 0 smelt abundance (Fig. 7a and 7b). Besides daphnid length also mean length of *B. coregoni* ($n = 12$, $r = 0.72$) correlated significantly with the onset of piscivory. A positive but non-significant relationship was found between age 0 smelt length over 5 cm and onset of piscivory (Fig. 7c). The inverse relation between daphnid length and age 0 smelt abundance was not significant ($n = 12$, $r = -0.55$, $0.05 < p < 0.10$).

Environmental data on the distribution of *Gammarus* spp. are lacking. In the northern part, *Gammarus* were observed as a food item in the southeast corner only. If arbitrarily these data had been split into those stations where *Gammarus* were found and those where they were not found, the onset of piscivory would have been at a greater length for those stations where *Gammarus* were present.

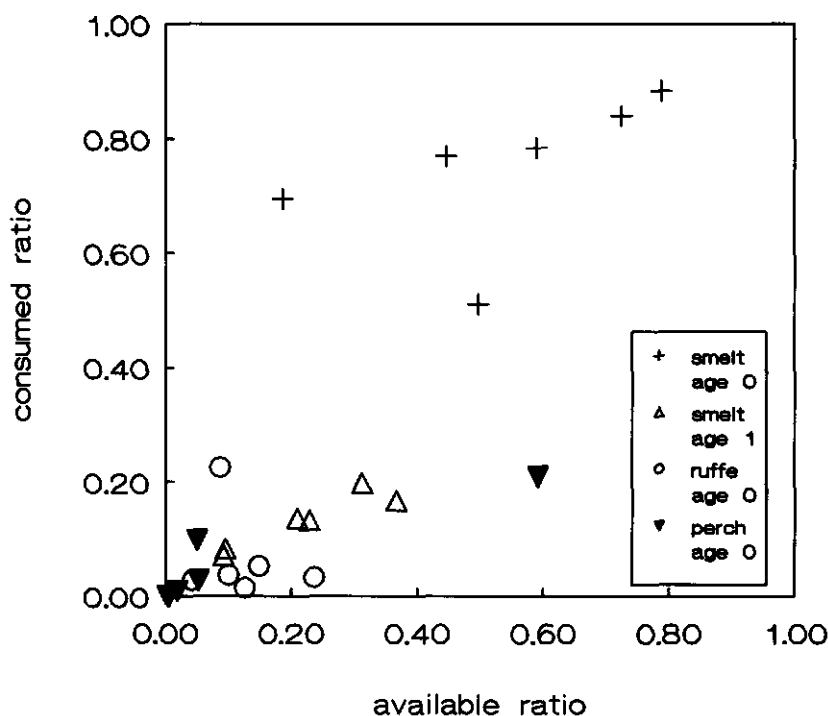


Fig. 8. Ratio between the frequency of occurrence of age 0 smelt, age 1 smelt, age 0 ruffe and age 0 perch and the frequency that one of these food items was observed in the stomachs of 13 to 30 perch versus the ratio between the specific and the total abundance of these food items in the lake. Data were combined for August and September, and represent both lake parts in 1987 - 1989.

Table 4. Abundance (number (1000 m trawling)⁻¹) and consumption (number of stomachs containing prey item) of age 0 prey fish by 13 to 30 cm perch at sampling site '13' in August and September 1989. Ivlev selectivity index, which is estimated per species and date, is $(r_i \cdot p_i) / (r_i + p_i)$ with r_i = ratio between the number of stomachs with a certain fish prey and the total number of stomachs with one of those fish prey and p_i = ratio between the abundance of that fish prey and the abundance of all four age 0 fish prey in the population.

| date | Abundance of prey fish | | | | Number of investigated stomachs | Stomachs with fish prey | | | | Ivlev selectivity index | | | |
|-------------------|------------------------|-------|-------|-------|---------------------------------|-------------------------|-------|-------|-------|-------------------------|-------|-------|-------|
| | age 0 | age 0 | age 0 | age 0 | | age 0 | age 0 | age 0 | age 0 | age 0 | age 0 | age 0 | age 0 |
| | perch | smelt | ruffe | roach | | perch | smelt | ruffe | roach | perch | smelt | ruffe | roach |
| 15 August 1989 | 410 | 968 | 1806 | 5 | 188 | 18 | 70 | 0 | 0 | 0.23 | 0.45 | -1.00 | -1.00 |
| 22 August 1989 | 1038 | 1097 | 948 | 28 | 499 | 23 | 102 | 1 | 1 | -0.30 | 0.39 | -0.95 | -0.07 |
| 14 September 1989 | 3052 | 1070 | 3313 | 1029 | 194 | 19 | 27 | 3 | 0 | 0.04 | 0.63 | -0.73 | -1.00 |

Selection of fish prey

Densities of age 0 smelt were always higher than those of age 1 smelt, age 0 ruffe and age 0 perch, except in the northern part in August and September 1989 when age 0 perch was the dominant species (Table 3). Their relative importance varied among years and parts of the lake, and coincided with their importance as a food item in the perch stomachs (Fig. 4).

To investigate whether perch feeds selectively on certain fish prey categories, ratios in the lake and in the stomachs were compared. As the four major fish prey categories mentioned above were found in stomachs of perch from 13 cm onwards, only these perch were used for comparison. Comparison of the relative importance of a fish prey category in the lake and in the perch stomachs showed that age 0 smelt appeared to be highly preferred (Fig. 8). The ratio of age 0 smelt varied in the lake from 0.19 to 0.79, while its importance as a food item varied from 0.51 to 0.88. The importance of the other fish prey was always less than 0.25. Additionally Fig. 8 shows that age 0 perch, age 0 smelt and age 1 smelt were more consumed when their relative availability was higher. This conclusion on fish prey preference is clouded by spatial differences in the relative importance of prey fish in the lake and by the varying number of stomachs investigated per site. Therefore, electivity indices were calculated according to Ivlev (1961) at one site ('13'), where in total 881 stomachs were investigated on three occasions in August and September 1989 (Table 4). In all cases age 0 smelt was the most preferred fish prey followed by age 0 perch. Age 0 ruffe and roach, although very abundant in the lake, were hardly found in the stomachs.

DISCUSSION

Percids show a large plasticity in their growth. Growth of perch in Lake IJssel is rapid as compared with the growth at other locations (Alm 1946; Deelder 1951; Shafi and Maitland 1971; Thorpe 1977). Fast growth of perch in Lake IJssel becomes most obvious at higher age when it has switched towards eating smelt. Growth in other Dutch waters (Deelder 1951) and in Sweden (Alm 1946) only became stunted at a higher age when suitable prey fish was absent.

The onset of piscivory for age 1 fish might be facilitated by fast growth of age 0 fish when summer temperatures were high and abundance was low. Growth of age 0 perch in lake IJssel and Windermere (LeCren 1958) correlate significantly with DD14. Water temperatures in Windermere (DD14 = 126-503 °C.d over the period 1934-1955) are generally lower than those in Lake IJssel (DD14 = 325-615 °C.d over the period 1966-1989) and the information on

effects of water temperature on growth from both lakes is complementary (Fig. 9). The intercept of the line suggests that growth occurs in both lakes at temperatures below 14°C. For the same reason, Craig (1980), proposed to use 8°C as the lower limit based on scale annulus formation studies by Holčík (1967 in Craig 1980). We have chosen 14°C to allow comparison with LeCren's (1958) data. Both lakes display a similar influence of water temperature on perch growth, and since perch stocks have varied largely in size the remainder of the variation might be caused by density-dependent processes.

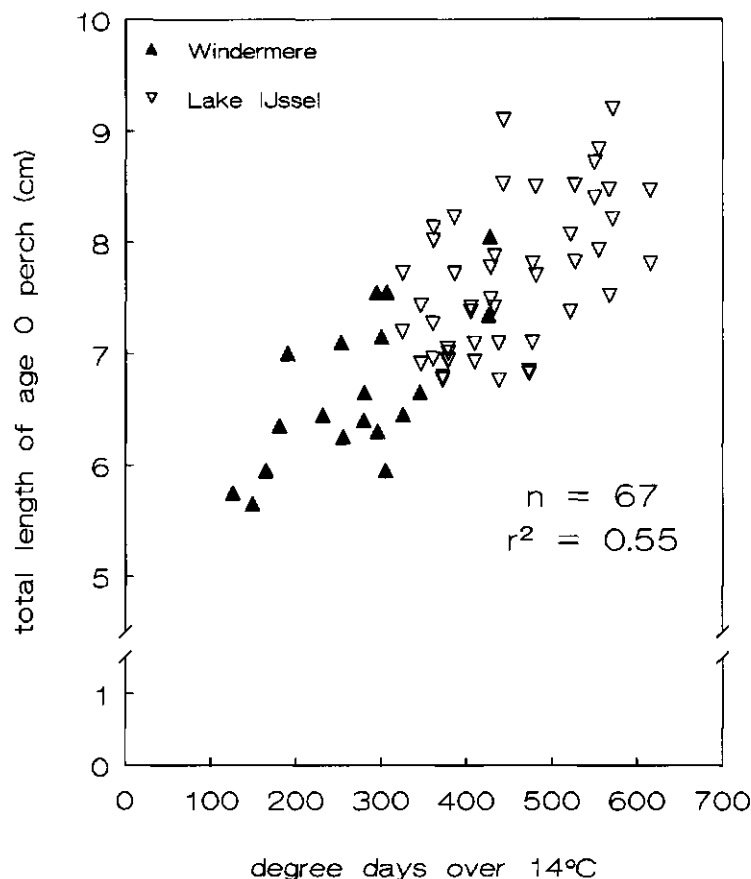


Fig. 9. Mean length of age 0 perch versus the water temperature expressed as the total yearly sum of degree days over 14°C. Data for Windermere are averages of age 0 male and female from LeCren (1958).

In Lake IJssel growth of age 0 was also influenced by age 0 densities, probably acting via the exploitation of the larger zooplankton species in the lake. In Oneida Lake, *Daphnia pulex* populations have persisted through late summer when young yellow perch were scarce and disappeared when age 0 were abundant. The latter resulted in a shift to alternate prey and retarded growth (Mills and Forney 1981, 1983). Growth differences have been illustrated in detail for year-classes [82] and [85]. Growth in the warm 1982 was faster than in the cold 1985. Growth of [82] was retarded in the southern part, where densities were higher than in the northern part. The large length of age 0 fish of [82] in the northern part has probably facilitated the onset of piscivory, allowing faster growth at age 1 as well. Unfortunately, no data were available on stomach contents in these years.

A general picture of the feeding behaviour of perch in Lake IJssel has been described by Willemsen (1977). Our study showed that feeding was flexible within the 3-years period. Perch is well known for its flexibility in feeding behaviour. Extremes vary between cannibalistic fingerlings of 18 - 28 mm preying on larvae of up to 13 mm (Spanovskaya and Grygorash 1977) and 25 cm adults feeding on zooplankton (Hartmann 1975; Klemetsen 1973). Macrofauna was the most important food item for yellow perch over 19 cm in Lac St. Louis (Fortin and Magnin 1972), and for 10-22 cm perch in brackish Tvärminne (Koli et al. 1988). We observed cannibalistic perch as small as 8 cm and perch containing zooplankton and chironomids in their stomachs as large as 27 cm. The major shift towards piscivory, however, occurred in the same range of 10 - 20 cm in Lake IJssel as observed in other waters (Windermere, Allen 1935, McCormack 1970; Lake Pääjärvi, Koli et al. 1988; Lake Opinicon, Keast 1977).

Age 0 perch in Lake IJssel probably never has become piscivorous, because mean length of age 0 perch was smaller than 10 cm in all years. The onset of piscivory in largemouth bass (Keast and Eadie 1985), pike (Frost 1954 in Keast 1985), pikeperch (Van Densen 1985b) and walleye, *Stizostedion vitreum*, (Cuff 1980) occurs generally at a younger age than in perch. This could be due to the slower growth of perch, because piscivory can be expected at a similar length for all these species (Chodorowska and Chodorowski 1975). However, according to Keast (1985), perch is classified as belonging to the "secondary piscivores, which are in no way structurally specialised for piscivory, other than in acquiring a large mouth with age".

Stunted growth of perch has been attributed both to food type and food availability. Perch has been known to prey size-selectively within species of zooplankton (Chabot and Maly 1986; Van Densen 1985a), invertebrates (Keast 1977) and fish (Knight et al. 1984; this study). Increasing prey sizes are reported to enhance growth (Confer and Lake 1987, Rask 1983), possibly

because the nutritional value of fish is higher than that of zooplankton and macrofauna (Keast and Eadie 1985). A high proportion of zooplankton in the diet of perch resulted in reduced growth (Boisclair and Leggett 1989; Hansson 1985). In Lauwersmeer fast growth was observed on a diet of chironomids and *Neomysis integer* (Willemsen 1977) and in Lake Volkerak on a diet of *Daphnia pulex* and *N. integer* (Houthuijzen et al. 000). In both areas the abundance of zooplankton and macrofauna was high after the original estuaries were dammed and had become freshwater lakes. Other studies indicated, that perch can attain a large length on a diet of daphnids and *Bythotrephes longimanus* (Klemetsen 1973; Hartmann 1975).

In Lake IJssel, stunted growth of perch appears to be primarily a result of food availability. Due to the heavy exploitation of the perch and pikeperch stock in Lake IJssel, the impact of these predators on the prey stocks is decreased. Prey fish are abundant and may over-exploit the zooplankton and possibly also the macrofauna. Indeed, mean length of the preferred daphnids were small compared to those found in Tjeukemeer, where daphnid length was inversely correlated with densities of planktivores (Van Densen 1985a). Zooplankton size in Oneida Lake decreased when the predator: prey fish ratio decreased (Mills et al. 1987). The faster growth of piscivorous perch in Lake IJssel thus might be a top-down effect caused by the commercial gill net fishery on predators, and hence the observed growth differences between piscivores and non-piscivores is than explained best by a food-limited growth of the non-piscivores.

Onset of piscivory led to bimodal length distributions of age 0 pikeperch (Van Densen 1985b) and largemouth bass (Timmons et al. 1980). For perch, LF-distributions became positively skewed in their second or third year. This skewness is partly due to sex-related growth differences, but distributions for males and females were skewed also. An initial difference in growth rate between males and females was amplified by a difference in feeding mode if only the larger, mainly female perch in the cohort became piscivorous during the growing season. If the whole age-group recruited to piscivory, it resulted in a smaller variance in the cohort LF-distribution and greater length by the end of the year. Although many authors cite that perch growth is enhanced by eating fish (Alm 1946; Deelder 1951; Sumari 1971), intra-cohort divergence of size distributions in this species to our knowledge only has been reported under artificial conditions (Chodorowski 1975). Our study showed that although the impact of food on size distributions of perch is not as dramatic as for pikeperch and largemouth bass, it significantly modifies the shape of size distributions. A practical consequence is that LF-analysis packages, e.g. MIX (MacDonald and Green 1988) and ELEFAN (Gayaniilo et al. 1989), are not suitable under these circumstances, because they are not capable of dealing with highly skewed

distributions. Studies on perch, therefore, should always include age determination, which is relatively easy in perch (LeCren 1947).

Zooplankton and probably also macrofauna densities and composition, and to a lesser extent prey fish availability, influenced the onset of piscivory. Prey fish availability can be expressed both by their length and abundance. A smaller size of age 0 smelt will make this fish prey more available. The mean length of age 0 smelt (3.6 cm) in the northern part in June 1987 is much smaller, while the onset of piscivory was at a greater length than the mean length of age 0 smelt in the southern part in September (6.1 cm). In our study the onset of piscivory is thus thought to be retarded by a high availability of zooplankton. Alewives (*Alosa pseudoharengus*) were also less piscivorous in Claytor Lake in early summer 1979 when zooplankton abundance was higher (Kohler and Ney 1980). In addition, the eutrophication of Lake Constance has resulted in higher zooplankton production which protects young perch being eaten by larger ones (Hartmann 1975).

Conclusive evidence cannot be given whether it is a lack or a scarcity of other food items which induces this switch towards *Gammarus* spp. rather than the presence of this amphipod at certain sites. In Oneida Lake frequency of occurrence of amphipods followed similar trends as their abundance in the environment suggesting that presence induces consumption, and cannibalism was lower at high densities of amphipods and large mean length of age 0 yellow perch (Tarby 1974). Although in Lake IJssel eating zooplankton and macrofauna was less profitable than eating fish, a higher availability of these alternative prey appeared to delay the onset of piscivory. Perch may be capable of switching towards piscivory at a smaller length, but may not doing so, because this demands a different feeding behaviour: as a planktivore or a macrobenthivore it can hunt individually, but as a piscivore it is reported to hunt in shoals surrounding prey fish and then attacking them (Thorpe 1977).

Mainly age 0 smelt are exploited by the Lake IJssel perch population. Perches between 10 and 15 cm are capable of eating age 0 ruffe and perch, but smelt is the most slender and spineless fish and therefore seems the easiest to grasp for perch which are just starting to eat fish. In western Lake Erie the slender clupeids were more selected by yellow perch than young yellow perch (Knight et al. 1984). Age 0 roach, although abundant in the lake in 1989, was hardly found in stomachs of perch despite its similar shape to smelt. Perch seems to have a poor ability to utilize small roach as a food resource, for reasons unknown (Persson 1986). Willemsen (1977) showed that ruffe is most frequently found in 31 - 45 cm perch, but perch over 30 cm are rare due to the intensive gill net fishery.

Prey fish availability and consumption were compared at one site, but estimates of prey fish densities could have suffered from varying vulnerability

to trawling. Abundance indices of ruffe varied considerably probably because catchability of this species in bottom trawls varied with water clarity (Buijse et al. 1992). Any underestimation of ruffe abundance would suggest even more strongly it is not preferred as prey. Trawl surveys could also have underestimated the abundance of smelt, because smelt is largely pelagic and trawls sample only the meter of water closest to the bottom. Removal of the weights of the ground rope, which made the trawl function more or less as a midwater trawl, did not result in a decline in the smelt catches, while those of other species declined substantially. A correction for the underestimated smelt biomass based on the assumption that smelt is homogeneously distributed over the water column would not alter the basic conclusion that age 0 smelt is preferred by perch. Ivlev indices would be lower but still positive. For the other species sampling the meter closest to the bottom probably yields the best area swept clear estimates.

Onset of piscivory does not influence survival of perch individuals as it does for obligatory piscivores like pikeperch (Buijse and Houthuijzen 1992; Van Densen 1985b) and largemouth bass (Wicker and Johnson 1987). This was already obvious from existence of old, slow-growing individuals in stunted populations of non-piscivorous perch (Alm 1946, Deelder 1951). In Lake IJssel, perch which did not become piscivorous in their second year would have made this switch at age 2 or even at age 3. The consequence of a postponed switch towards eating fish acts more on growth than on survival in Lake IJssel, because age 1 and older perch are hardly preyed upon by larger perch and pikeperch. The onset of piscivory could have an indirect effect on the perch stock, because a large stock of piscivorous perch will reduce survival of younger congeners (Alm 1952; Mills and Hurley 1990; Staub and Krämer 1991), but in Lake IJssel smelt will buffer this cannibalism to a large extent.

Two processes, food competition by non-piscivores and variation in temperature, appeared to be of main importance for the growth of perch in Lake IJssel. Our study revealed the following conclusions: (1) growth of perch does not become stunted at higher age due to the presence of smelt; (2) growth of age 0 perch is density-dependent and positively influenced by high summer temperatures; (3) fast growth of age 0 facilitates the onset of piscivory at age 1; (4) low availability of zooplankton accelerates the onset of piscivory at age 1 or 2, thus food competition between age 0 and age 1 perch could induce piscivory of the latter; (5) intra-cohort onset of piscivory can enhance initial growth differences between males and females; (6) the increased growth does not influence survival directly like for pikeperch (Buijse and Houthuijzen 1992; Van Densen 1985b) and largemouth bass (Wicker and Johnson 1987), but can induce mortality among offspring by cannibalism.

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REFERENCES

- Aggus, S.M., and G.V. Elliott. 1975. Effects of cover and food on year-class strength of largemouth bass. p. 317-322. In R.H. Stroud, and H. Clepper [ed.] Black bass biology and management. Sport Fishing Institute, Washington D.C., USA.
- Allen, K.R. 1935. The food and migration of the perch (*Perca fluviatilis* L.) in Windermere. *J. Anim. Ecol.* 4: 264-273.
- Alm, G. 1946. Reasons for the occurrence of stunted fish populations with special regard to perch. Meddn. St. Unders. -o. ForsAnst. Sotvatt Fisk. 25: 1-146.
- Alm, G. 1952. Year class fluctuations and span of life of perch. Rep. Inst. Freshw. Res. Drottningholm 33: 17-38.
- Boisclair, D., and W.C. Leggett. 1989. Among-population variability of fish growth: II. Influence of prey type. *Can. J. Fish. Aquat. Sci.* 46: 468-482.
- Buijse, A.D., W.L.T. van Densen, and L.A. Schaap. 000. Year-class strength of perch (*Perca fluviatilis* L.) and pikeperch (*Stizostedion lucioperca* (L.)) in relation to stock size, water temperature and wind in Lake IJssel, The Netherlands, 1966-1989. (chapter 3)
- Buijse, A.D., and R.P. Houthuijzen. 1992. Piscivory, growth and size-selective mortality of age 0 pikeperch, *Stizostedion lucioperca* (L.). *Can. J. Fish. Aquat. Sci.* 49: 000-000.
- Buijse, A.D., L.A. Schaap, and T.P. Bult. 1992. The influence of water clarity on the catchability of six freshwater fish species in bottom trawls. *Can. J. Fish. Aquat. Sci.* 49: 000-000.
- Chabot, F., and E.J. Maly. 1986. Variation in the diet of yellow perch (*Perca flavescens*) in a Quebec reservoir. *Hydrobiologia* 137: 117-124.
- Chodorowska, W., and A. Chodorowski. 1975. Substitution d'elements de la diete chez les alevins de poissons carnassiers. *Verh. Internat. Verein. Limnol.* 19: 2556-2562.
- Chodorowski, A. 1975. Formation de populations bimodales chez les alevins de poissons carnassiers. *Verh. Internat. Verein. Limnol.* 19: 2546-2555.
- Confer, J.L., and G.J. Lake. 1987. Influence of prey type on growth of young yellow perch (*Perca flavescens*). *Can. J. Fish. Aquat. Sci.* 44: 2028-2033.
- Craig, J.F. 1980. Growth and production of the 1955 to 1972 cohorts of perch, *Perca fluviatilis* L., in Windermere. *J. Anim. Ecol.* 49: 291-315.

- Cuff, W.R. 1980. Behavioral aspects of cannibalism in larval walleye, *Stizostedion vitreum*. Can. J. Zool. 58: 1504-1507.
- Deelder, C.L. 1951. A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. Hydrobiologia 3: 357-378.
- Densen, W.L.T. Van. 1985a. Feeding behaviour of major 0+ fish species in a shallow, eutrophic lake (Tjeukemeer, the Netherlands). J. Appl. Ichthyol. 1: 49-70.
- Densen, W.L.T. Van. 1985b. Piscivory and the development of bimodality in the size distribution of 0+ pikeperch (*Stizostedion lucioperca* L.). J. Appl. Ichthyol. 1: 119-131.
- Densen, W.L.T. Van, W.G. Cazemier, W. Dekker, and H.G.J. Oudelaar. 1990. Management of the fish stocks in Lake IJssel, The Netherlands, p. 313-327. In W.L.T. Van Densen, B. Steinmetz, and R.H. Hughes [ed.] Management of freshwater fisheries. Proceedings of a symposium organized by the European Inland Fisheries Advisory Commission, Göteborg, Sweden, 31 May - 3 June 1988. PUDOC, Wageningen.
- Fentener van Vlissingen, A. 1988. Voedselsamenstelling en -selectie bij baars, snoekbaars en spiering in het IJsselmeer in 1987. (Food composition and selection of perch, pikeperch and smelt in IJsselmeer in 1987). Department of Fish Culture and Fisheries, Agricultural University Wageningen. MSc-thesis no. 1275. 59 p. (in Dutch with English summary)
- Fortin, R., and E. Magnin. 1972. Quelques aspects qualitatifs et quantitatifs de la nourriture des perchaudes, *Perca flavescens* (Mitchill), dans la Grande Anse de L'île Perrot, au Lac Saint-Louis. Ann. Hydrobiol. 3: 79-91.
- Gayanilo, F.C., Jr., M. Soriano, and D. Pauly. 1989. A draft guide to the compleat ELEFAN. ICLARM Software 2. International Center for Living Aquatic Resources Management, Manila, Philippines. 70 p.
- Hansson, S. 1985. Local growth differences in perch (*Perca fluviatilis* L.) in a Baltic archipelago. Hydrobiologia 121: 3-10.
- Hartmann, J. 1975. Der Barsch (*Perca fluviatilis*) im eutrophierten Bodensee. Arch. Hydrobiol. 76: 269-286.
- Houthuijzen, R.P. 1989. Voedsel en groei van juveniele snoekbaars, baars en spiering in het IJsselmeer in 1987 en 1988 (Food and growth of juvenile pikeperch, perch and smelt in IJsselmeer in 1987 and 1988). Agricultural University Wageningen, Department of Fish Culture and Fisheries. MSc-thesis no. 1277. 30 p. + annexes. (in Dutch with English summary)
- Houthuijzen, R.P., J.J.G.M. Backx, and A.D. Buijse. 000. Rapid growth and early maturation of Eurasian perch (*Perca fluviatilis* L.) in a recently freshened lake. (unpublished manuscript)
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press., New Haven, Connecticut.
- Jeziarska, B. 1974. The effect of various type of food on the growth and chemical composition of the body of perch (*Perca fluviatilis* L.) in laboratory conditions. Pol. Arch. Hydrobiol. 21: 467-479.
- Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Env. Biol. Fish. 2: 53-70.
- Keast, A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. Env. Biol. Fish. 12: 119-129.

- Keast, A., and J.Mca. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. *Trans. Am. Fish. Soc.* 114: 204-213.
- Klemetsen, A. 1973. Pelagic, plankton-eating perch. *Astarte* 6: 27-33.
- Knight, R.L., F.J. Margraf, and R.F. Carline. 1984. Piscivory by walleyes and yellow perch in Western Lake Erie. *Trans. Am. Fish. Soc.* 113: 677-693.
- Kohler, C., and J.J. Ney. 1980. Piscivory in a land-locked alewife (*Alosa pseudoharengus*) population. *Can. J. Fish. Aquat. Sci.* 37: 1314-1317.
- Koli, L., M. Rask, M. Viljanen, and E. Aro. 1988. The diet of perch, *Perca fluviatilis* L., at Tvärminne, northern Baltic Sea, and a comparison with two lakes. *Aqua Fennica* 18: 185-191.
- Köpke, U., H. Schultz, R. Jarchow, U. Hornig, and J. Penig. 1988. An investigation of the food consumption in perch (*Perca fluviatilis*) in the Bautzen reservoir. *Limnologica* 19: 37-43.
- LeCren, E.D. 1947. The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. *J. Anim. Ecol.* 16: 188-204.
- LeCren, E.D. 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years, with special reference to the effects of temperature and changes in population density. *J. Anim. Ecol.* 27: 287-334.
- Macdonald, P.D.M. and Green, P.E.J., 1988. User's Guide to program MIX: An interactive program for fitting mixtures of distributions. Ichthus data systems, Hamilton, Ontario, Canada. 60 p.
- McCormack, J.C. 1970. Observations on the food of perch (*Perca fluviatilis* L.) in Windermere. *J. Anim. Ecol.* 39: 255-265.
- Mills, C.A., and M.A. Hurley. 1990. Long-term studies on the Windermere populations of perch (*Perca fluviatilis*), pike (*Esox lucius*) and Arctic charr (*Salvelinus alpinus*). *Freshw. Biol.* 23: 119-136.
- Mills, E.L., and J.L. Forney. 1981. Energetics, food consumption, and growth of young yellow perch in Oneida lake, New York. *Trans. Am. Fish. Soc.* 110: 479-488.
- Mills, E.L., and J.L. Forney. 1983. Impact on *Daphnia pulex* of predation by young yellow perch in Oneida Lake, New York. *Trans. Am. Fish. Soc.* 112: 154-161.
- Mills, E.L., D.M. Green, and A. Schiavone Jr. 1987. Use of zooplankton size to assess the community structure of fish populations in freshwater lakes. *N. Am. J. Fish. Manag.* 7: 369-378.
- Mills, E.L., R. Sherman, and D.S. Robson. 1989. Effect of zooplankton abundance and body size on growth of age-0 yellow perch (*Perca flavescens*) in Oneida Lake, New York, 1975-86. *Can. J. Fish. Aquat. Sci.* 46: 880-886.
- Nagieć, M. 1977. Pikeperch (*Stizostedion lucioperca*) in its natural habitats in Poland. *J. Fish. Res. Board Can.* 34: 1581-1585.
- Neuman, E. 1976. The growth and year-class strength of perch (*Perca fluviatilis* L.) in some Baltic Archipelagoes, with special reference to temperature. *Rep. Inst. Freshw. Res. Drottningholm* 55: 51-70.
- Persson, L. 1986. Effect of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). *Ecology* 67: 355-364.

- Rask, M. 1983. Differences in growth of perch (*Perca fluviatilis* L.) in two small forest lakes. *Hydrobiologia* 101: 139-144.
- Rask, M., and J. Raitaniemi. 1988. The growth of perch, *Perca fluviatilis* L., in recently acidified lakes of southern Finland - a comparison with unaffected waters. *Arch. Hydrobiol.* 112: 387-397.
- Schlumpberger, W. 1962. Überblick über die Probleme der Zanderwirtschaft in den Küstengewässern der Deutschen Demokratischen Republik. *Z. f. Fisch. deren Hilfswiss.* 10: 715-720.
- Shafi, M., and P.S. Maitland. 1971. The age and growth of perch (*Perca fluviatilis* L.) in two Scottish lochs. *J. Fish Biol.* 3: 39-57.
- Shelton, W.L., W.D. Davies, T.A. King, and T.J. Timmons. 1979. Variation in growth of the initial year class of largemouth bass in West Point Reservoir, Alabama and Georgia. *Trans. Am. Fish. Soc.* 108: 142-149.
- Spanovskaya, V.D., and V.A. Grygorash. 1977. Development and food of age-0 Eurasian perch (*Perca fluviatilis*) in reservoirs near Moscow, USSR. *J. Fish. Res. Board Can.* 34: 1551-1558.
- Staub, E., and A. Krämer. 1991. Grossversuch mit 28mm-Netzen zur Befischung der Wachstumsverzögerten Barschkohorte 1988. *SVA/IBK*. 27 p. + appendices.
- Sumari, O. 1971. Structure of the perch populations of some ponds in Finland. *Ann. Zool. Fennici* 8: 406-421.
- Tarby, M.J. 1974. Characteristics of yellow perch cannibalism in Oneida Lake and the relation to first year survival. *Trans. Am. Fish. Soc.* 103: 462-471.
- Thorpe, J. 1977. Synopsis of biological data on the perch, *Perca fluviatilis* Linnaeus, 1758 and *Perca flavescens* (Mitchill, 1814). *FAO Fish. Synop.* no. 113. vii + 138 p.
- Timmons, T.J., W.L. Shelton, and W.D. Davies. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama and Georgia. *Trans. Am. Fish. Soc.* 109: 176-186.
- Wicker, A.M., and W.E. Johnson. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. *Trans. Am. Fish. Soc.* 116: 264-271.
- Willemsen, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. *J. Fish. Res. Board Can.* 34: 1710-1719.

Appendix 1. Total number of examined stomachs (per size-class and sampling period) and percentage empty stomachs (per size-class) of 6 to 36 cm perch in the northern (a) and southern (b) part of Lake Issel from 1987 to 1989 and frequency of occurrence (c) of a certain food item per size-class of perch (data from all sampling periods and both lake parts combined).

| a. total number of examined stomachs and percentage empty stomachs in the northern part | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----|----|----|----|----|-----|----|----|----|----|----|--|---|--|
| size-class (cm total length) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| period | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | | | |
| June 1987 | 10 | 73 | 126 | 63 | 18 | 176 | 309 | 141 | 59 | 41 | 14 | 5 | 7 | 5 | 5 | 5 | 18 | 9 | 11 | 6 | 7 | 3 | 3 | | | | | | | | | | | |
| August 1987 | 5 | 53 | 231 | 197 | 137 | 246 | 256 | 172 | 118 | 57 | 33 | 22 | 6 | 11 | 25 | 31 | 29 | 38 | 24 | 26 | 9 | 4 | 4 | 7 | | | | | | | | | 1 | |
| September 1987 | 10 | 93 | 208 | 132 | 203 | 237 | 191 | 132 | 67 | 52 | 34 | 18 | 6 | 8 | 9 | 12 | 10 | 15 | 9 | 1 | 1 | 1 | 1 | | | | | | | | | | | |
| June 1988 | 1 | 1 | 2 | 17 | 22 | 28 | 36 | 33 | 19 | 20 | 17 | 16 | 6 | 5 | 1 | | | | | | | | | | | | | | | | | | | |
| August 1988 | 2 | 6 | 25 | 44 | 34 | 60 | 143 | 151 | 134 | 68 | 61 | 45 | 40 | 57 | 61 | 42 | 5 | 4 | 5 | 4 | 2 | | | | | | | | | | | | | |
| September 1988 | 3 | 8 | 4 | 31 | 45 | 57 | 62 | 101 | 129 | 131 | 99 | 82 | 89 | 95 | 83 | 38 | 18 | 7 | 1 | | | | | | | | | | | | | | | |
| June 1989 | 10 | 4 | 1 | 2 | 4 | 12 | 10 | 25 | 29 | 16 | 25 | 13 | 13 | 17 | 6 | 8 | 4 | 1 | | | | | | | | | | | | | | | 1 | |
| August 1989 | 2 | 8 | 33 | 123 | 149 | 120 | 54 | 27 | 51 | 75 | 99 | 103 | 68 | 75 | 58 | 47 | 32 | 30 | 19 | 8 | 1 | | | | | | | | | | | | | |
| September 1989 | 5 | 8 | 25 | 43 | 53 | 49 | 19 | 12 | 11 | 29 | 49 | 46 | 37 | 37 | 24 | 20 | 10 | 8 | 7 | | | | | | | | | | | | | | | |
| total | 10 | 76 | 142 | 143 | 377 | 672 | 717 | 881 | 989 | 875 | 688 | 422 | 351 | 316 | 315 | 345 | 331 | 248 | 178 | 142 | 99 | 88 | 51 | 20 | 6 | 9 | 1 | 2 | | | | | 1 | |
| empty (%) | 7 | 10 | 10 | 29 | 37 | 28 | 36 | 43 | 43 | 46 | 41 | 50 | 45 | 43 | 40 | 42 | 38 | 36 | 49 | 46 | 41 | 39 | 55 | 50 | 56 | 100 | 50 | | | | | | | |

| b. total number of examined stomachs and percentage empty stomachs in the southern part | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|----|-----|-----|----|----|----|-----|-----|-----|-----|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|-----|----|----|----|--|--|--|
| size-class (cm total length) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| period | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | | | |
| June 1987 | 8 | 105 | 110 | 14 | 8 | 30 | 48 | 33 | 18 | 6 | 7 | 11 | 8 | 8 | 8 | 4 | 7 | 4 | 6 | 5 | 2 | 4 | 1 | 1 | | | | | | | | | | |
| August 1987 | 1 | 6 | 66 | 26 | 6 | 10 | 9 | 16 | 17 | 11 | 9 | 4 | 13 | 4 | 2 | 1 | 9 | 8 | 8 | 3 | 2 | 3 | 3 | 1 | 1 | | | | | | | | | |
| September 1987 | 15 | 43 | 25 | 23 | 14 | 10 | 17 | 17 | 14 | 12 | 13 | 7 | 14 | 12 | 13 | 7 | 7 | 10 | 13 | 10 | 13 | 8 | 2 | 2 | 3 | | | | | | | | | |
| June 1988 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| August 1988 | 1 | 4 | 6 | 12 | 21 | 38 | 35 | 30 | 28 | 9 | 12 | 11 | 6 | 18 | 12 | 24 | 15 | 8 | 5 | 4 | 3 | 1 | | | | | | | | | | | | |
| September 1988 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| June 1989 | 6 | 7 | 5 | 1 | 1 | 4 | 12 | 16 | 31 | 46 | 4 | 5 | 6 | 4 | 3 | 2 | 6 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | | | | | | | | | | |
| August 1989 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| September 1989 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| total | 8 | 105 | 117 | 28 | 90 | 88 | 137 | 166 | 158 | 138 | 102 | 66 | 49 | 70 | 57 | 75 | 56 | 84 | 66 | 48 | 38 | 25 | 13 | 10 | 8 | 1 | 1 | | | | | | | |
| empty (%) | 13 | 28 | 20 | 18 | 13 | 24 | 43 | 37 | 34 | 42 | 40 | 47 | 33 | 31 | 30 | 39 | 29 | 45 | 44 | 41 | 35 | 45 | 64 | 46 | 40 | 25 | 100 | 100 | | | | | | |

Appendix 1. continued

c. frequency of occurrence of food items (total number of stomachs)
size-class (cm total length)

| food item | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 |
|-------------------|---|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----|----|----|----|----|----|----|----|----|----|----|----|
| zooplankton | 6 | 84 | 159 | 135 | 155 | 260 | 328 | 351 | 258 | 119 | 44 | 26 | 9 | 6 | 7 | | 2 | | 1 | | | | 1 | | | | | | | | |
| chironomids | 7 | 17 | 9 | 39 | 15 | 26 | 42 | 38 | 28 | 7 | 1 | 2 | 1 | 2 | 10 | 6 | 3 | 2 | 4 | 1 | | | 1 | | | | | | | | |
| Gammarus spp. | 1 | 1 | 4 | 4 | 12 | 30 | 61 | 89 | 122 | 104 | 60 | 38 | 20 | 10 | 6 | 3 | 2 | 4 | 1 | | | | | | | | | | | | |
| Neomysis integer | | | 1 | 5 | 54 | 32 | 19 | 10 | 12 | 3 | 6 | 8 | 8 | 5 | 2 | 5 | 7 | 7 | 4 | 1 | 3 | | | | | | | | | | |
| age 0 smelt | | | | 1 | | 14 | 34 | 59 | 155 | 263 | 299 | 240 | 166 | 103 | 114 | 116 | 134 | 111 | 108 | 70 | 42 | 31 | 25 | 12 | 6 | 5 | 2 | | | | |
| age 1 smelt | | | | | | | | 1 | 6 | 8 | 13 | 15 | 10 | 13 | 24 | 13 | 32 | 41 | 31 | 27 | 26 | 18 | 17 | 9 | 3 | 5 | 3 | | | | |
| age 0 perch | 1 | 2 | 1 | 1 | | | | 2 | 5 | 12 | 14 | 14 | 6 | 10 | 9 | 8 | 15 | 13 | 13 | 14 | 10 | 6 | 6 | 3 | | | 1 | | | | |
| age 1 perch | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| age 0 ruffe | 1 | | | | | | | 1 | 5 | 6 | 10 | 7 | 8 | 4 | 7 | 7 | 15 | 11 | 9 | 5 | 5 | 3 | 5 | 4 | 3 | | | 1 | | | |
| age 1 ruffe | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| age 0 roach | | | | | | | | | 1 | 2 | 4 | | | | 1 | | | | | 1 | | | | | | | | | | | |
| age 0 bream | | | | | | | | | | | | | | 1 | | | | | | 1 | | | | | | | | | | | |
| age 0 pikeperch | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| bullhead | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| eel | | | | | | | | | 1 | | | | | | | | | | | 1 | | | | | | | | | | | |
| unidentified fish | | | 2 | 6 | 9 | 21 | 41 | 76 | 136 | 128 | 98 | 73 | 61 | 63 | 64 | 73 | 55 | 51 | 47 | 26 | 18 | 17 | 13 | 4 | 1 | | | | | | |
| other | | | | | | 1 | 1 | 1 | 2 | 5 | 4 | 3 | 2 | | 3 | 4 | 1 | 5 | 1 | | | | | | | | | | | | |

Chapter 6

A SIZE- AND AGE-STRUCTURED SIMULATION MODEL FOR EVALUATING MANAGEMENT STRATEGIES IN A MULTISPECIES GILL NET FISHERY.

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ABSTRACT

A size- and age-structured simulation model is presented for evaluation of management strategies for a multispecies gill net fishery, using a commercial gill net fishery for pikeperch (*Stizostedion lucioperca*) and perch (*Perca fluviatilis*) as an example. The model takes size distributions within age-groups into account. Growth for each sex is determined by length and temperature and dispersion in size distributions is controlled by the 'fractional boxcar train' method. The model is applied to evaluate the integrated short-term and long-term effects of management measures such as mesh size regulations, fishing effort limitations and combinations of both on the biomass, the size- and age-structure of the stock and of the yield. Changes in yield during the transitional period after a management measure has been implemented, can be quantified.

INTRODUCTION

In managing a fishery, the consequences of different management strategies have to be evaluated. Some consequences are easily deduced on the basis of classical fish stock assessment models as formulated by e.g. Beverton and Holt (1957) and Ricker (1958). In many cases these classical dynamic pool models are based on the concept of age-structured populations, and are simplified by assuming constant mortality and knife-edge recruitment to the fishery. More modern dynamic pool models include age-dependent mortality and gradual recruitment to the fishery (Pitcher and Hart, 1982; Jacobson and Taylor, 1985). Natural mortality is, however, more related to size than to age. For instance, predation, as the most important cause of natural mortality (Peterson and Wroblewski, 1984) is essentially size-selective (Dekker, 1983).

Fishing gears are also size-selective rather than age-selective, and considerable bias can be introduced by the assumption of knife-edge recruitment at a certain age to a fishery. This is particularly true for heavily exploited populations and for short-lived tropical species, where the selection range of the catching gear covers a large fraction of the size-distribution of the population. Although this problem can be overcome by applying empirical sigmoid selection curves in age-structured models as done for the Samar Sea multispecies trawl fishery (Silvestre and Soriano, 1988), an age- and size-structured model will show the consequences much more clearly (Sissenwine, 1977). Size-structured models are particularly suited for gill net fisheries, which exploit only a small proportion of population's size distribution.

Steady-state size-structured models have been used to evaluate management strategies for gill net fisheries on lake whitefish, *Coregonus clupeaformis* (Berkes and Gönenc, 1982), and on perch, *Perca fluviatilis* (Staub et al., 1987). Berkes and Gönenc (1982) note that their steady-state model is limited by not taking into account the progressive change in population structure due to the fishery-induced size-selective mortality. Dynamic age-structured models have been used to evaluate short-term as well as long-term effects (Hightower and Grossman, 1987), but dynamic size-structured models will probably provide a more realistic description.

In the present study a size- and age-structured dynamic pool model is described for scanning the effects of management alternatives for the multispecies gill net fishery on pikeperch, *Stizostedion lucioperca*, and perch in Lake IJssel ('IJsselmeer'), a 182,000 ha shallow eutrophic freshwater lake in The Netherlands. The stock of pikeperch is heavily exploited and, according to Willemsen (1977, 1983) and Van Densen et al. (1990), subject to growth-overfishing. Since large numbers of females are already caught at age 2 when they are just maturing (Willemsen, 1983), there is even an imminent danger of

recruitment overfishing. The perch stock, however, shows no signs of overexploitation. Since perch grow more slowly than pikeperch (Willemsen 1977), fishermen foresee a permanent decrease in the perch catches if management measures, such as mesh size and effort regulations or a combination of both, are implemented to rationalise the exploitation of pikeperch. The model has been applied to investigate the integrated effects of a number of management options.

MATERIAL AND METHODS

Description of the Lake IJssel fishery

The mean yields of pikeperch and perch in the gill net fishery in the period 1980-1989 were 0.76 and 3.17 kg.ha⁻¹ amounting to 10.6% and 22.2% of the value of the total yield (Dfl 13,350,000) from Lake IJssel respectively. On average, the value per kg of pikeperch is twice the value of perch. The gill net fishing season lasts from July 1 until March 15 and the legal minimum mesh size of the gill nets is 101 mm stretched mesh. Legal minimum landing sizes of pikeperch and perch are 42 and 22 cm total length respectively. Total mortalities were estimated at 81% for age 2 pikeperch and at 67% for age 4 perch in the beginning of the 1970s (Willemsen, 1977). Although the number of fishing companies has decreased by half over the last 20 years, the total fishing mortality increased because overall more gill nets were used (Dekker, 1991). Also, the fishermen switched from multifilament to monofilament gill nets, which are two times as efficient for perch and one and a half times for pikeperch (Schaap, 1987). A similar increase in efficiency was observed for lake whitefish (*Coregonus clupeaformis*) in Lake Huron where catch comparisons showed that monofilament gill nets were 1.8 times as efficient as multifilament nets (Collins, 1979). There is no limitation on the number of gill nets allowed per fishing company, but the fishing effort has been restricted to some extent by a ban on gill net fishing during Saturdays and Sundays.

Model and parameters

Model structure

The general structure of the model is depicted in the relational diagram (Fig. 1). A list of symbols used is given in Table 1. The model includes two species, each of which consists of eight age-groups, and is based on 100 size-classes (cm). Fish recruit to the stock at age 1 (January 1st). The initial size distribution of the age 1 fish is described by a normal distribution. Growth rates are based

on a von Bertalanffy growth equation for each sex, which is modified to reflect inter-annual variations in the growth rate. The dispersion in the size distribution of an age-group as it grows older is simulated by applying the 'fractional boxcar train' method (Goudriaan and Van Roermund, 1989). At January 1st, every age-group switches to the next, the oldest one being removed from the model. Natural mortality is assumed to be length-dependent and decreases to a constant value for fish above a certain size. Fishing mortality is a function of the number of companies fishing with gill nets, the length of the fishing season and the mesh size of the gill nets. The model has been written in CSMP III (Continuous System Modelling Program: IBM, 1975) using a fixed time step of 1 day. This is a conservative choice taking into account that 1/4 of the smallest time constant, being 25/4 days, is small enough to justify the assumption that the highest rate does not change materially over time (De Wit, 1982).

Table 1. List of abbreviations used in the relational diagram.

| | |
|--------|---|
| a | = age-class (yr) |
| co | = companies (numbers) |
| d | = day number of the year (-) |
| F | = fishing mortality rate (d^{-1}) |
| FM | = fishing mortality (numbers. d^{-1}) |
| FR | = fraction to control dispersion (-) |
| l | = length-class (cm) |
| le | = fish length in a unexploited population (cm) |
| M | = natural mortality rate (d^{-1}) |
| N | = number of fish (arbitrary units) |
| NM | = natural mortality (number. d^{-1}) |
| R | = recruitment (arbitrary units.yr $^{-1}$) |
| S | = selectivity of gill net (-) |
| season | = open or closed (1/0) |
| shifta | = transfer of all fish to next age-class at January 1 st |
| shiftl | = transfer of fraction FR of total number to next length-class |
| T | = temperature ($^{\circ}C$) |
| vbgf | = growth according to von Bertalanffy (cm. d^{-1}) |
| Y | = yield (kg) |

Parameter estimates

Parameters are based on data collected on pikeperch and perch in Lake IJssel in the period 1966-1989. Certain parameters for pikeperch, which could not be derived from the stock of Lake IJssel because little fishery-independent data could be collected due to the high exploitation rate there, are based on data from the pikeperch stock in Tjeukemeer, a 2,000 ha shallow eutrophic lake in

relative yield estimates per age-group are insensitive to year-to-year variation in recruitment, as long as growth and mortality are density-independent. Therefore, to evaluate the effect of possible management strategies, only the ratio of recruitment in the two species is required. Since 1966, bottom trawl surveys in autumn have been carried out to estimate the year-class strength of pikeperch and perch, indexed as the number of age 0 per standard haul. During the period 1966-1987 the average ratio in recruitment of pikeperch and perch was 1:8. This ratio is used (in arbitrary units) in the model.

Table 2. Mean total length, L (cm), and standard deviations, s (cm), at age (yr) for populations of male and female pikeperch and perch in Lake IJssel in the case without exploitation. Lengths at age were calculated using the von Bertalanffy growth parameters L_{∞} , k and t_0 .

| | age 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | L_{∞} cm | k yr^{-1} | t_0 yr |
|---------------------|----------|------|------|------|------|------|------|------|--------------------|-------------------------|-------------|
| pikeperch σ | | | | | | | | | | | |
| L | 15.0 | 30.1 | 41.8 | 50.8 | 57.7 | 63.1 | 67.2 | 70.4 | 81.2 | 0.26 | 0.21 |
| s | 1.7 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | | | |
| pikeperch φ | | | | | | | | | | | |
| L | 14.8 | 30.1 | 42.4 | 52.4 | 60.5 | 67.0 | 72.2 | 76.5 | 94.4 | 0.21 | 0.20 |
| s | 1.7 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | | | |
| perch σ | | | | | | | | | | | |
| L | 7.1 | 13.2 | 18.3 | 22.5 | 26.0 | 28.9 | 31.3 | 33.3 | 42.7 | 0.19 | 0.05 |
| s | 0.6 | 1.3 | 2.0 | 2.5 | 2.9 | 3.2 | 3.4 | 3.7 | | | |
| perch φ | | | | | | | | | | | |
| L | 6.8 | 13.0 | 18.4 | 23.1 | 27.1 | 30.7 | 33.7 | 36.4 | 54.2 | 0.14 | 0.04 |
| s | 0.6 | 1.3 | 2.0 | 2.5 | 3.0 | 3.4 | 3.7 | 4.0 | | | |

Growth

In the model the daily growth in length is assumed to be dependent on length and on temperature and is specific to sex. Growth is formulated according to the von Bertalanffy growth function:

$$\frac{\delta L}{\delta t} = k_d [L_{\infty} - L_{t-1}] \quad (1)$$

where:

L_{t-1} = total length (cm)

t = time (d)

k_d = temperature-dependent daily growth constant (d^{-1})

L_{∞} = theoretical length at infinite age (cm)

Lengths at age 1 serve as a starting value for L_{t-1} .

The resulting mean lengths-at-age and standard deviations of male and female perch and pikeperch are given in Table 2. Pikeperch grow faster than perch and females faster than males. Parameter estimates are based on information on mean length at successive ages. For pikeperch, Willemsen (1983) estimated potential growth ("theoretical growth in unexploited situation") for the Lake IJssel stock. The differences in growth rate between sexes are based on data from Tjeukemeer. For perch no data on potential growth were available. Growth parameters for perch are based on back-calculations with the aid of opercula (Le Cren, 1947) of age 1 to 5 perch, which were caught during bottom trawl surveys in Lake IJssel in 1987 (Pet, 1988).

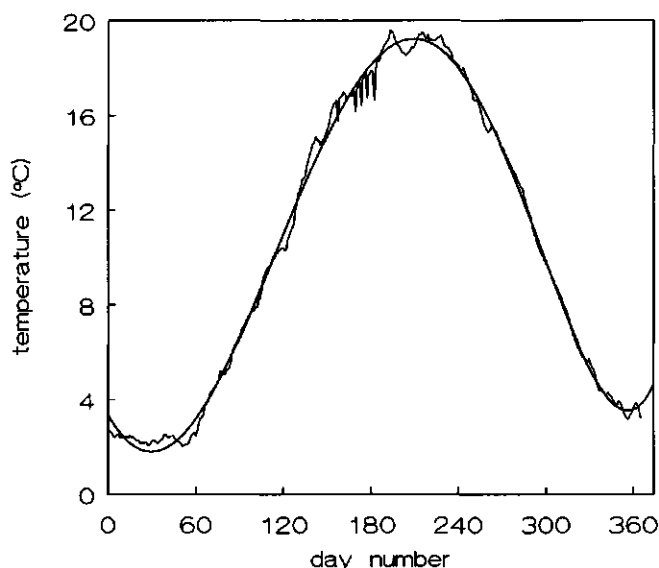


Fig. 2. Mean daily water temperature in Lake IJssel in the period 1971-1986. A fifth order polynomial function is fitted to the data: $T (^{\circ}\text{C}) = 3.39 - 1.11 \cdot 10^{-1} \cdot d + 2.04 \cdot 10^{-3} \cdot d^2 - 2.94 \cdot 10^{-6} \cdot d^3 - 2.18 \cdot 10^{-8} \cdot d^4 + 4.62 \cdot 10^{-11} \cdot d^5$; where d = day number; $n = 365$; $r = 0.998$.

Pikeperch and perch grow if the water temperature is above 14°C (Le Cren 1958; Willemsen 1978). The average daily water temperatures in Lake IJssel from 1971 to 1986 show that this minimum temperature for growth was exceeded from May 15 until September 29 (Fig. 2). Therefore, growth is made a function of water temperature and in this way the von Bertalanffy growth function is seasonalised. The growth rate k is assumed to be linearly related with the water temperature above 14°C . This seems reasonable because water temperature in Lake IJssel never exceeded 21°C , which is well below the

temperature for the physiological optimum of pikeperch (27.3 °C) or perch (25.4 °C) (Hokanson, 1977). For convenience, a fifth order polynomial is fitted through the annual cycle of temperature, and daily temperatures in the model are calculated with this polynomial. From the sum of degree-days above 14°C (453 °C.d) divided by the number of days per year (365 d), which equals 1.24°C, the daily growth constant k_d was calculated according to:

$$k_d = \frac{(T_d - 14)}{1.24} * \frac{k}{365} \quad (2)$$

where:

d = day number (1 to 365)

T_d = water temperature (°C)

k = yearly growth constant (yr⁻¹)

Size structure per age-group

The initial length-frequency distribution of the recruiting age-group was described by a normal distribution function according to which the fish were distributed among length-classes. Recruitment was split into males and females, assuming an initial sex ratio of 1:1. Thus, the initial length-frequency distribution for each species and sex is given by equation:

$$N(L) = \frac{1}{2} * \frac{R}{s_1 \sqrt{2\pi}} * e^{-\frac{(L-L_1)^2}{2s_1^2}} * W \quad (3)$$

where:

$N(L)$ = calculated initial frequency in length-class L

L = mid-length of length-class (cm)

R = recruitment (arbitrary units)

s_1 = standard deviation at age 1 (cm)

L_1 = mean length at age 1 (cm)

W = width of the length-class (cm)

The number 2 in the denominator accounts for the sex ratio.

The standard deviations of the mean lengths at age indicate an increasing divergence in the length frequency distribution with age (Table 2). This divergence can be simulated with the 'fractional boxcar train' method, by which dispersion in a length-frequency distribution of an age-group is controlled. The method is based on a fractional, repeated shift of the number of fish in a length-class: a fraction FR of the frequency in a length-class is transferred to the next length-class as soon as the increase in length, based on the summation of the daily growth according to (1), equals a proportion FR of the width of the length-class. FR is a function of the mean length and the standard deviation of the consecutive age-groups:

$$FR = 1 - \left(\frac{s_{a+1}^2 - s_a^2}{L_{a+1} - L_a} \right) \quad (4)$$

where:

L = mean total length of an age-group, calculated with equation (1) (cm)

s = standard deviation of the size distribution of an age-group (cm)

a = age (yr)

After transfer, the summation function of daily growth is reset to zero.

Length-weight relationship

An allometric function is used to describe the relation between body length L (cm) and body weight W (g) of pikeperch and perch. For pikeperch $W = 0.00425 * L^{3.2}$ and for perch $W = 0.0104 * L^{3.13}$ is used.

Size at maturity

Data on the size at maturity are needed for the calculation of the spawning stock biomass. The range for which the fraction of mature females increases from 0 to 1 is 40-50 cm for pikeperch and 14-23 cm for perch. A simple linear relationship is assumed between the fraction of mature females per length-class and fish length.

Natural mortality

Natural mortality has been estimated for age 0 and 1 pikeperch and age 0 to 2 perch based on the numerical abundance of pikeperch and perch age-groups in bottom trawl surveys in Lake IJssel. Daily instantaneous natural mortality

rate M_d (d^{-1}) is described as a function of the body length L (cm): $M_d = 0.0047 * e^{-0.079 * L}$ and $0.0049 * e^{-0.087 * L}$ for pikeperch smaller than 27 cm and perch smaller than 25 cm respectively. The natural mortality rate for larger fish is assumed to be constant ($0.2 \text{ y}^{-1} = 0.00055 \text{ d}^{-1}$).

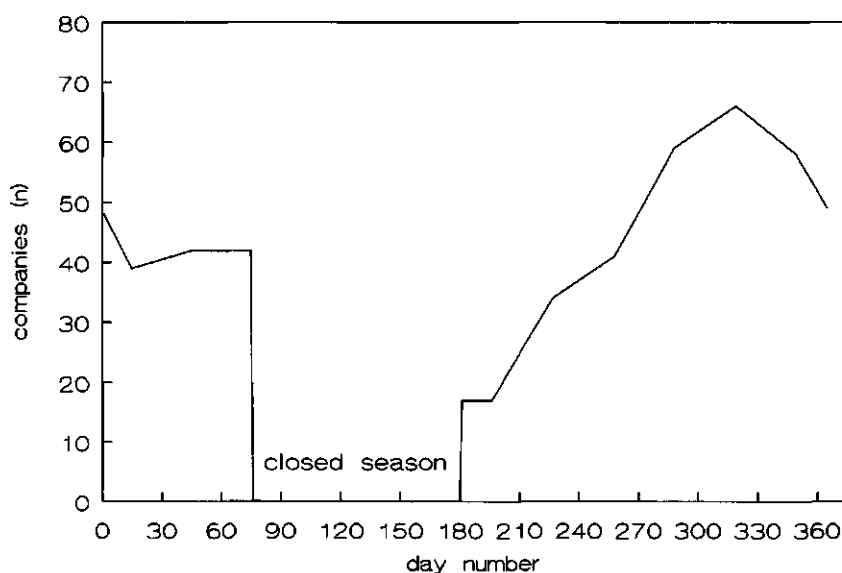


Fig. 3. Intra-seasonal variation in the number of companies fishing with gill nets based on monthly averages over the period 1969-1982 which were linearly interpolated between the middle of two months (Anonymous 1969-1982). The gill net season is closed from March 15 to July 1.

Fishing mortality

The daily instantaneous fishing mortality rate (F_d) per length-class is assumed to be a function of the mean daily fishing mortality for the length-class optimally caught in a gill net (F_{op}) and the selectivity (S) per length-class, which is a fraction (0 to 1) of F_{op} (5). Within a year, the fishing mortality also varies due to the number of companies fishing with gill nets, which is zero if the season is closed (Fig. 3).

$$F_{d,i}(L) = F_{op} * S_i(L) * \frac{C_d}{C_m} \quad (5)$$

where:

$F_{d,i}$ = fishing mortality per length-class per day (d^{-1})

F_{op} = mean daily fishing mortality during the open season for the length-class optimally caught in a gill net (d^{-1})

d = day number

i = i^{th} distinct mesh size used in the gill net fishery (1 to n)

S_i = selectivity per length-class of a gill net with a certain mesh size (0 to 1)

L = total length (cm)

C_d = number of companies fishing with gill nets on a given day

C_m = mean number of companies fishing with gill nets during the open season

F_{op} varies proportionally with fishing effort and was used to simulate year-to-year variations in fishing effort. Total yearly instantaneous fishing mortality rate (F_y) per age-group is the summation of daily fishing mortalities of all length-classes of an age-group:

$$F_y(A) = \sum_{d=1}^{365} \sum_{L=1}^{100} \sum_{i=1}^n F_{d,i}(L) \quad (6)$$

where:

A = age-group (yr)

F_y = fishing mortality per age-group per year (yr^{-1})

n = number of distinct mesh sizes used in the gill net fishery

In this way it is possible to simulate the outcome of gill net fisheries with varying combinations of mesh sizes and fishing effort per mesh size.

Gill net selectivity

The selectivity of gill nets for pikeperch is based on data from Van Densen (1987), who calculated a length-dependent selection curve according to the method of Holt (1963). This selection curve was transformed into a selection curve as a function of the maximum girth: mesh perimeter ratio, because this gives a more realistic description. The selectivity of gill nets for perch is based on studies made by McCombie and Berst (1969) on yellow perch, *Perca flavescens*, which has a very similar morphology to perch (Thorpe, 1977). The maximum girth G (cm) is related to the total length L (cm) of the fish, for

pikeperch, by $G = 0.58 * L - 3.51$ and for perch, by $G = 0.81 * L - 2.26$. The selectivity S is described as a normal distribution function of the maximum girth of the fish and the mesh size of the gill net and varies between 0 and 1:

$$S_i(L) = e^{-\frac{(\frac{G(L)}{2 \cdot m} - OP)^2}{2s_{op}^2}} \quad (7)$$

where:

S_i = selectivity per length-class

L = total length (cm)

G = maximum girth (cm)

m = mesh size (cm stretched mesh)

OP = ratio of maximum girth: mesh perimeter ($= 2 \cdot m$) for the optimum of the selection curve

s_{op} = standard deviation of the selection curve

For pikeperch, $OP = 1.22$ and $s_{op} = 0.15$, and for perch a normal distribution was fitted through the data of McCombie and Berst (1969) resulting in $OP = 1.20$ and $s_{op} = 0.12$. The resulting selection curves for the two species in 101 mm and in 140 mm stretched mesh gill nets are presented in Fig. 4. These selectivity curves broaden with increasing mesh size.

Calibration of the fishing mortality

The gill net fishery on pikeperch and perch in Lake IJssel in the period 1974-1983 was used as a reference point for evaluating management strategies. The fishermen mostly used gill nets with 101 mm stretched mesh. The estimated yearly instantaneous fishing mortality rate F_y was 1.27 yr^{-1} (72%) for age 3 pikeperch, based on cohort analysis of catches of the year-classes 1971 to 1980 in the period 1974 to 1983. For age 5 perch fishing mortality was 1.05 yr^{-1} (65%) for the year-classes 1969 to 1978 in the same period (unpublished data). F_{op} was calibrated to simulate these yearly fishing mortalities for both species.

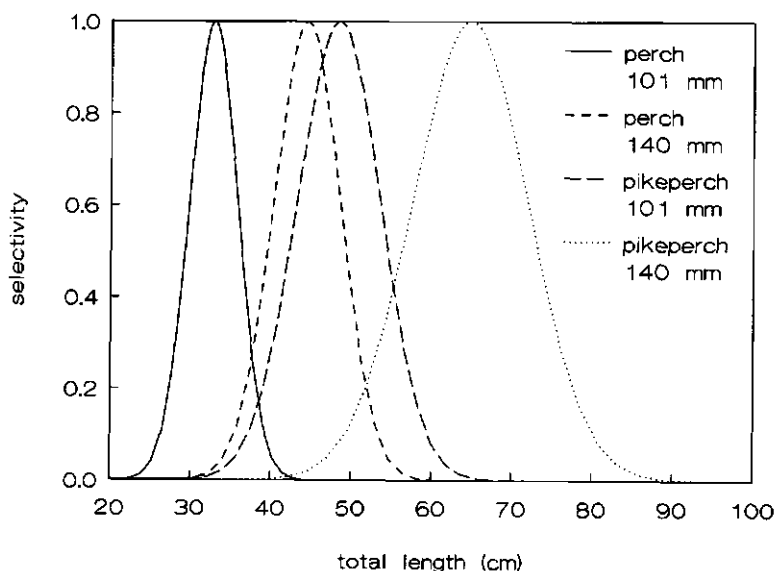


Fig. 4. Selectivity of 101 and 140 mm (stretched mesh) gill nets for pikeperch and perch (see text).

RESULTS

Validation

The model has been used to calculate and evaluate effects of various management measures on the yield and stock of pikeperch and perch. At first a comparison was made between model outcome and observations made on the pikeperch and perch yield and stock.

The length-frequency distribution of the simulated yield and the length-frequency distribution of the actual yield as observed at the fish auction during the ten-years reference period are presented in Fig. 5. The choice of the parameters in the simulation model for the gill net selectivity and the exploitation rate, as based on cohort analysis, yielded a length-frequency distribution for perch similar to the one observed at the fish auction. For pikeperch, the simulated length frequency is bimodal with modes for age 2 and 3 fish. The observed frequency distribution was unimodal, probably due to the effect of year-to-year differences in growth, which 'flattened out' the bimodal pattern. The model predicts a considerable proportion of the catch to be below the legal minimum landing size (42 cm), which suggests that discarding occurs on a relatively large scale.

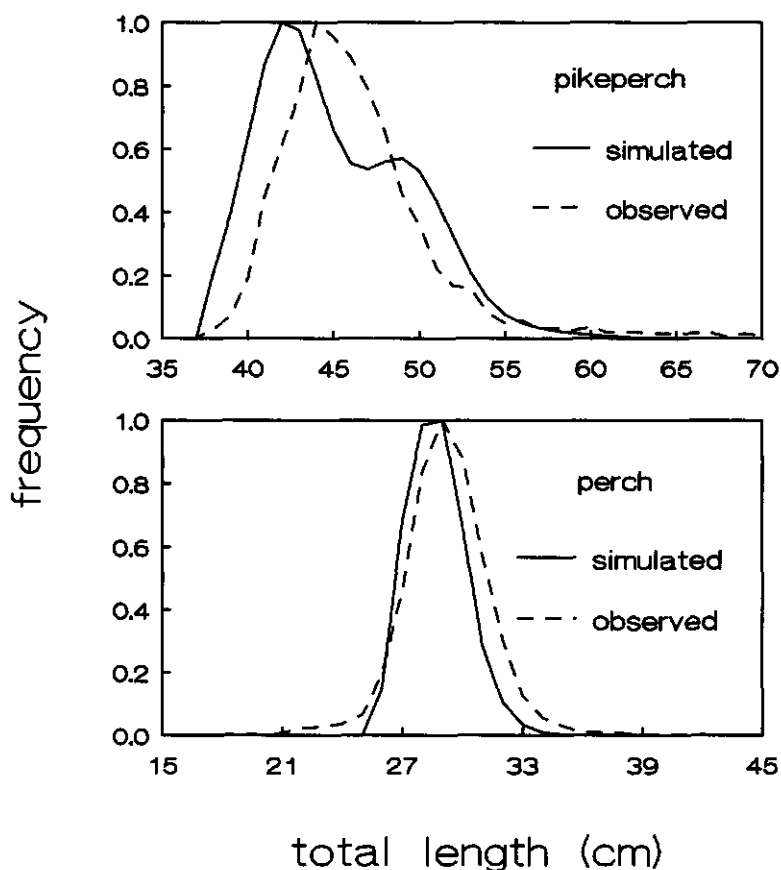


Fig. 5. Observed (the mean during the reference period 1974-1983) and simulated length-frequency distributions of pikeperch and perch catches in 101 mm stretched mesh gill nets.

The gill net selectivity appears to have had a most pronounced size-selective impact on the population structure of perch. The mean length at age observed in the catch was always larger than the mean length observed in the stock (Fig. 6). Thus, the gill net fishery appears to selectively exploit the larger perch in every age-group. Simulated mean lengths at age were always higher for the unexploited (Table 2) than for the exploited population (Table 3). The selective impact of the gill nets is also illustrated by the decrease of the standard deviation in the exploited situation. Apparent growth of the observed and simulated exploited stock almost ceased after age 4 due to the size-selective removal of larger perch (Fig. 6). The observed mean lengths were, however,

about 3 cm larger than the simulated ones. This might indicate that the growth parameters used for perch underestimate potential growth.

Pikeperch quickly grow through the selection range of 101 mm gill nets. The age 2 fish are exploited on the right-hand (larger) side of their size distribution, while age 4 and older fish were selectively exploited on the left-hand (smaller) side (Tables 2 and 3). Mean lengths in the simulated exploited and unexploited stocks did not differ by more than 1.8 cm. Observations of mean length at age in the stock were not available and a comparison between observed and simulated growth could therefore not be made.

The observed yields over the period 1974-1983 were 2.35 and 3.42 kg.ha⁻¹ for pikeperch and perch respectively. In the present version, the model does not provide yield in terms of kg.ha⁻¹, because recruitment indices are in arbitrary units. However, the ratio between the pikeperch and perch yields can be compared, which for the reference period resulted in a somewhat lower ratio (1.28) than observed (1.46) (Table 4).

Table 3. Simulated mean length, L (cm), and standard deviations, s (cm), at age (yr) of male and female pikeperch and perch in a population, which has been exploited with 101 mm gill nets during the reference period (see text for further explanation).

| | age 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|-------------|----------|------|------|------|------|------|------|
| pikeperch ♂ | | | | | | | |
| L | 29.9 | 40.3 | 49.0 | 57.0 | 63.5 | 67.6 | 70.6 |
| s | 2.6 | 2.5 | 2.7 | 2.7 | 2.5 | 2.5 | 2.5 |
| pikeperch ♀ | | | | | | | |
| L | 29.8 | 40.9 | 51.0 | 59.8 | 67.0 | 72.0 | 76.0 |
| s | 2.6 | 2.5 | 2.7 | 2.6 | 2.5 | 2.5 | 2.5 |
| perch ♂ | | | | | | | |
| L | 12.6 | 18.2 | 22.7 | 24.8 | 25.8 | 26.2 | 26.3 |
| s | 1.3 | 2.0 | 2.3 | 2.1 | 1.8 | 1.6 | 1.5 |
| perch ♀ | | | | | | | |
| L | 12.4 | 18.0 | 22.9 | 25.2 | 26.2 | 26.6 | 26.7 |
| s | 1.2 | 2.0 | 2.3 | 2.0 | 1.7 | 1.5 | 1.3 |

Management options for the Lake IJssel gill net fishery

The model was applied to evaluate the effects of four possible management strategies which were considered to represent realistic management options. The effects of the different management measures on the yield of pikeperch and perch are shown on a yearly basis during a transitional period until stabilisation in Fig. 7. Detailed information on the size and age composition of the yield after stabilisation is given Figs. 8 and 9 respectively.

Since recruitment in the model reflects the observed ratio between the two species, and reference exploitation rates were taken over the same period, changes in the yield and the stock of both species can be compared simultaneously after implementation of a management measure. Consequently, yield and (spawning) stock of both species are given as percentage of the stock biomass of pikeperch under the exploitation rate during the reference period (Table 4).

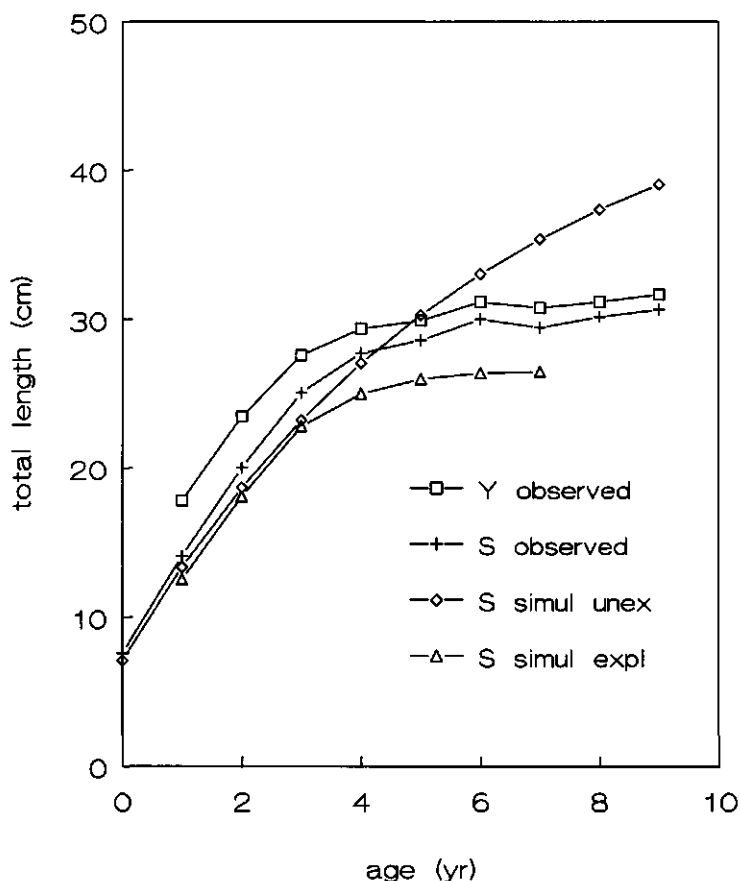


Fig. 6. Mean length at age of perch as observed in the stock (S) and yield (Y) in Lake IJssel over the period 1970-1988 and as simulated in an unexploited and in an exploited stock.

Table 4. Effects of management options in respect of mesh size (MS), effort (f) and length of season, on the yield (Y), stock biomass (SB) and spawning stock biomass (SSB) of pikeperch and perch. Y, SB and SSB of both species are given as percentages of the initial pikeperch SB; values between brackets are percentages of the initial Y and SSB for each species separately (see text for further explanation).

Pikeperch

| management option | MS mm | f % | open season | Y | SB | SSB |
|-------------------|-------|-----|----------------------|---------|-----|----------|
| Initial situation | 101 | 100 | 1 July - 15 March | 58 | 100 | 19 |
| 1 | 120 | 100 | 1 July - 15 March | 76(132) | 127 | 18(93) |
| 2 | 101 | 25 | 1 July - 15 March | 35(61) | 343 | 130(672) |
| 3 | 101 | 100 | 1 October - 15 March | 55(96) | 143 | 35(183) |
| 4 { | 101 | 25 | 1 July - 15 March | 29(50) | 136 | 22(112) |
| | 140 | 100 | | 49(84) | | |

Perch

| management option | MS mm | f % | open season | Y | SB | SSB |
|-------------------|-------|-----|----------------------|---------|-----|---------|
| Initial situation | 101 | 100 | 1 July - 15 March | 74 | 152 | 43 |
| 1 | 120 | 100 | 1 July - 15 March | 87(119) | 268 | 90(210) |
| 2 | 101 | 25 | 1 July - 15 March | 81(110) | 202 | 63(145) |
| 3 | 101 | 100 | 1 October - 15 March | 77(105) | 173 | 45(104) |
| 4 { | 101 | 25 | 1 July - 15 March | 80(109) | 199 | 61(141) |
| | 140 | 100 | | 2(1) | | |

Option 1. Increase of legal minimum mesh size from 101 to 120 mm

The yield of pikeperch increases, after a reduction of 23% in the first season, to a 32% higher yield after three to four seasons (Fig. 7). The pikeperch stock increases by 25%, whereas the spawning stock decreases slightly (Table 4). An increase in mesh size to 120 mm results in large reductions of 87 and 29 % of the perch yield during the first two seasons, but the yield stabilises after six years at a 20% higher level. The perch stock increases by 76% and the spawning stock by 110%. Due to the increase in mesh size, the size- and age-structure of the yield changes (Fig. 8 and 9). The number of age-groups in the yield stays the same, but the fish are about one year older.

Option 2. Reduction of fishing effort by 75 %

A 75% reduction in the number of gill nets has a negative effect on the total yield of pikeperch. After two to three seasons with a 50-60% lower yield, the yield stabilises at about 60% of the former level (Fig. 7). The pikeperch stock increases by more than 200% and the spawning stock by more than 500%. For perch, the yield stabilises after a decline of 42% during the first year, at a 10% higher level after four to six years. The perch stock and spawning stock

increase by 33% and 50% respectively. For both species the yield is more evenly distributed over the age-groups than in the original situation (Fig. 9).

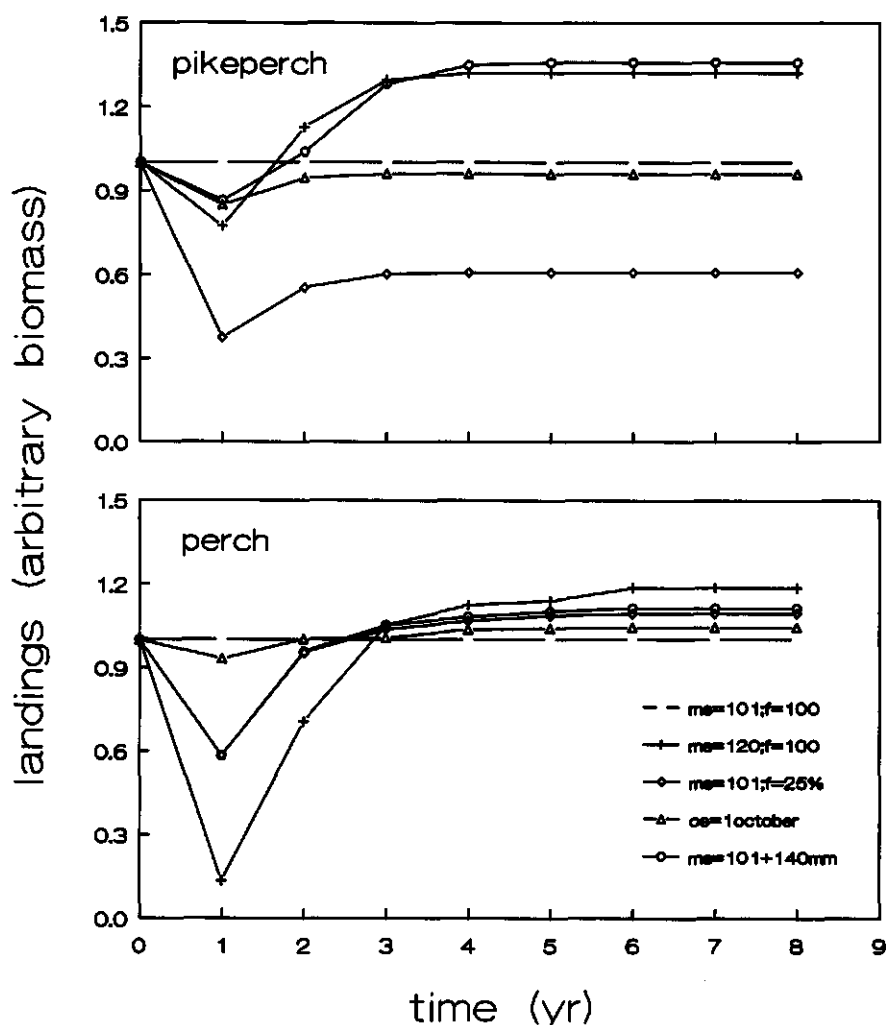


Fig. 7. Development in the yield of pikeperch and perch, relative to the initial situation ($ms=101\text{mm}$; $f=100\%$), in the first 8 years after implementation of four different management options (see also text). ms = mesh size (mm stretched mesh); f = relative fishing effort (%); os = opening of the fishing season.

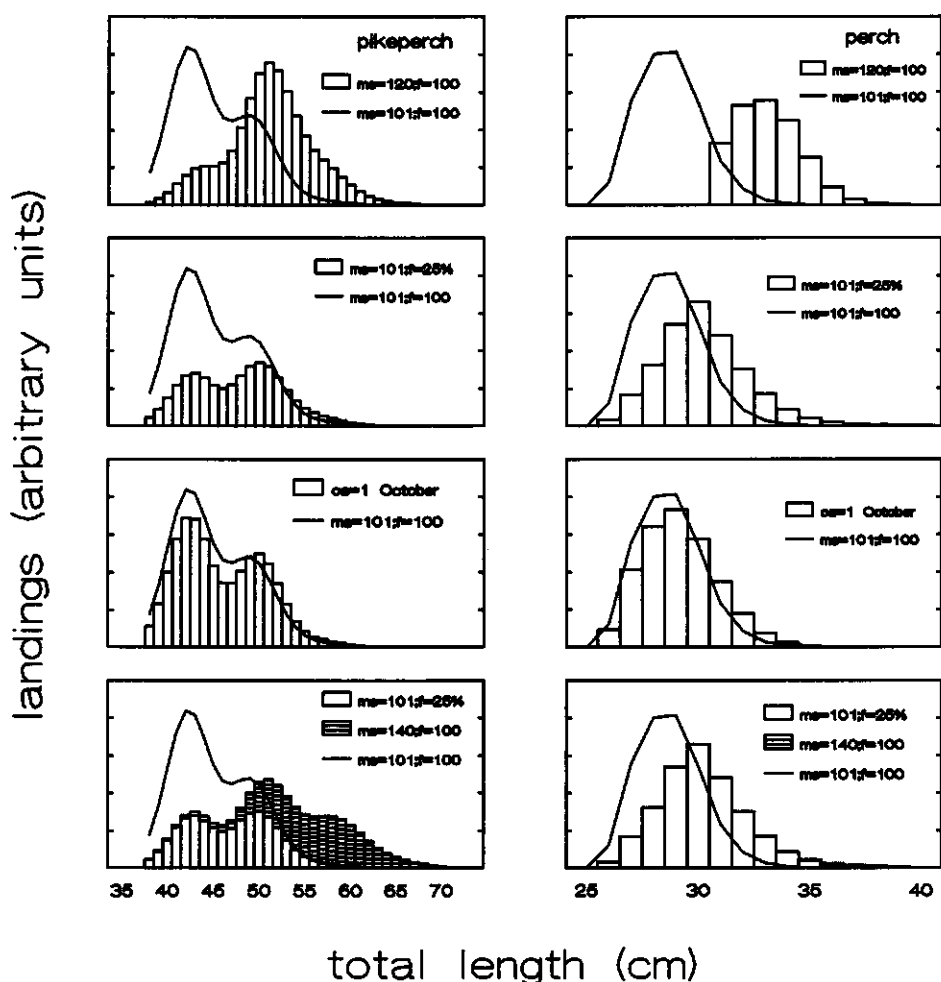


Fig. 8. Length-frequency distributions of the yield of pikeperch and perch. Line indicates the situation during the reference period; bars indicate the length composition after implementation of management measures. ms = mesh size (mm stretched mesh); f = relative fishing effort (%); os = opening of the season.

Option 3. Extension of the closed season to 1 October

Fishing effort can also be reduced by extending the period in which the fishery is closed e.g. less fishing days during the week or a shortening of the open season. However, it should be noted that fishermen might respond by setting more nets so that the effect of the measure is lost. A postponement of

the start of the fishing season from 1st July to 1st October has been suggested in order to utilise fully the growing season and to reduce, at least temporarily, the fishing effort. In the simulation the numbers of companies fishing during the remainder of the year was as given in Fig. 4.

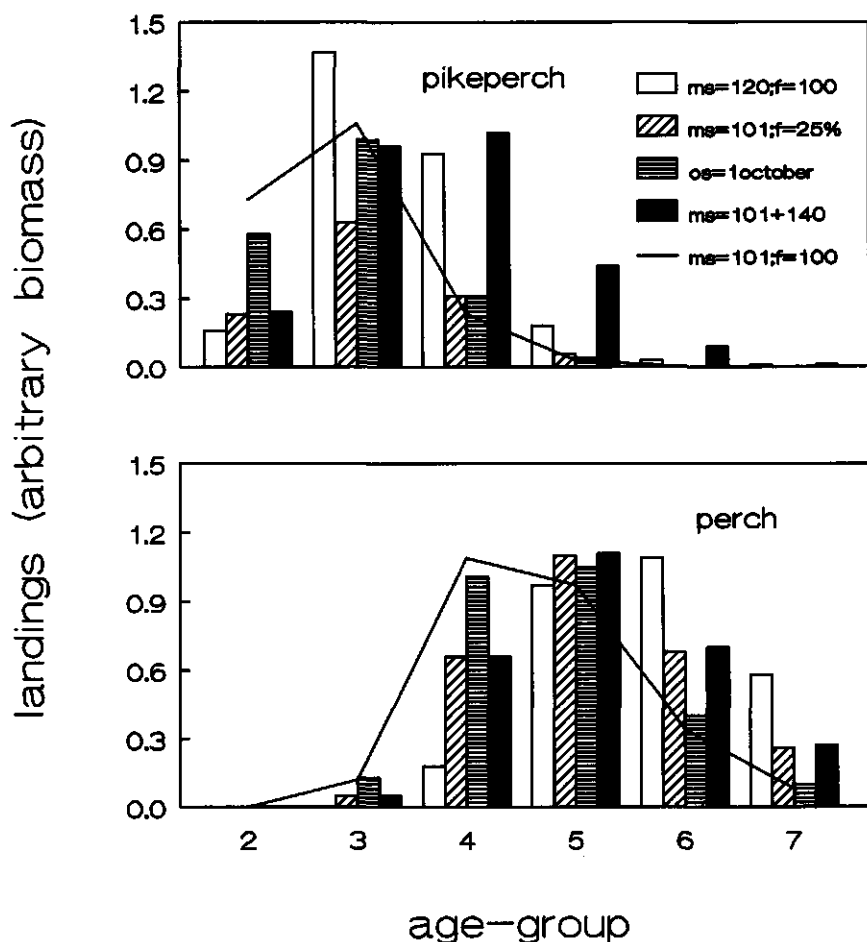


Fig. 9. Age-frequency distributions of the yield of pikeperch and perch. Line indicates the situation during the reference period; bars indicate the age composition after implementation of management measures. ms = mesh size (mm stretched mesh); f = relative fishing effort (%); os = opening of the season.

Shortening of the open season has the most pronounced effect on the (spawning) stock biomass of pikeperch; the yield of both species remained close

to the former level. For pikeperch the portion of age 2 fish in the yield decreases while that of age 4 fish increases. The pikeperch stock and spawning stock increase by 43 and 83% respectively. The increase in biomass of perch is much less.

Option 4. 101 and 140 mm gill nets with 75 % effort reduction of 101 mm nets

Management of a multispecies fishery will always try to find a compromise between the optimum exploitation rates for the most important individual species, depending on species-related differences in growth and mortality rates. In Lake IJssel, the choice of a minimum mesh size of 101 mm is based on the length at maturity of pikeperch. Short-term losses are large for perch when mesh size is increased, whereas a reduction in fishing effort might result in a permanent lower yield of pikeperch as illustrated by option 2. Therefore, a compromise was sought by allowing a certain number of 101 mm gill nets in order to catch the perch, but to keep this number low in order not to overexploit the pikeperch stock. In addition a number of 140 mm gill nets is allowed in order to catch the surviving pikeperch, which have spawned several times.

In this model, the effect of using gill nets with different mesh sizes simultaneously can easily be evaluated. The option comprises a 75% effort reduction for 101 mm gill nets, and the introduction of 140 mm gill nets with an effort equal to the effort practised with 101 mm gill nets during the reference period. The yield of pikeperch in the 101 mm gill nets is comparable to the catch after implementing option 2 (Table 4). The additional yield in the 140 mm gill nets results in a higher total yield after two years. Furthermore, the decline in the yield of pikeperch after one year is only 14%. After four to five years the yield stabilises at 34% above the reference level. The stock and spawning stock are raised by 36% and 12%, respectively. The age composition of the yield shifts to a dominance of age 3 and 4 instead of age 2 and 3 fish (Fig. 9). In general, the yield has a more diverse age composition than is the case with other management measures. As perch is seldom caught in 140 mm gill nets, its yield and stock size are comparable with those after implementation of option 2.

Size- versus age-structured models

The results of our size-structured model were compared with an age-structured version of the same model. In the age-structured version, all fish of the same age have the same length, which corresponds with the calculations based on the von Bertalanffy growth parameters (Table 2). The size-structure

within age-groups is therefore not modified by the fishery. The gill net selectivity was estimated by using mean length-at-age in equation (7).

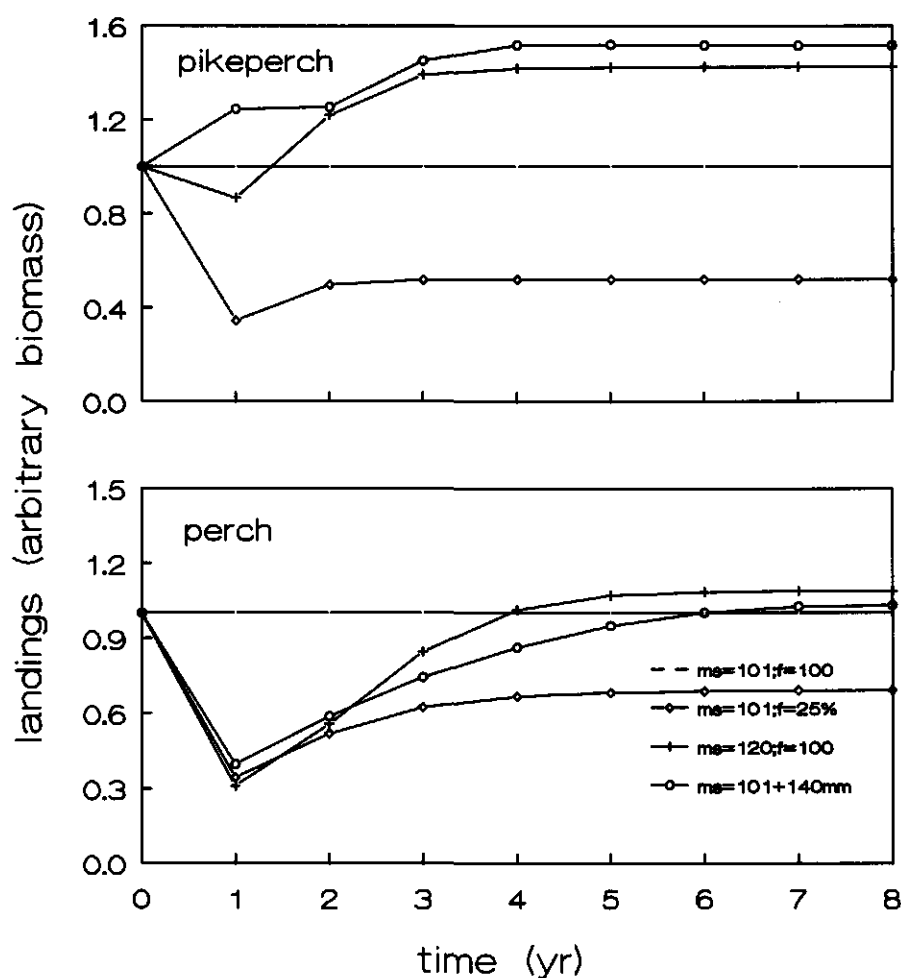


Fig. 10. Development in the yield of pikeperch and perch, relative to the initial situation ($ms=101\text{mm}$; $f=100\%$) and not accounting for size-selective processes, in the first 8 years after implementation of three different management options (see also text). ms = mesh size (mm stretched mesh); f = relative fishing effort (%).

Especially for perch, large differences in the total yield and the age composition of the yield are found between the size-structured (Fig. 7 and 9) and age-structured versions of the model (Fig. 10 and 11): the decline after

increasing the minimum legal mesh size to 120 mm was smaller for the age-structured version; a considerable amount of perch is landed by 140 mm gill nets; the age-structured model predicts a permanent reduction in the yield of perch if only the effort of 101 mm gill nets is reduced. Dominant age-groups in the yield of perch were about one year older in the age-structured than in the size-structured version. In the age-structured version, the ultimate gain of pikeperch when the options 1 and 4 were applied was slightly higher and the ultimate loss in the case of option 2 was slightly more, than in the size-structured model. Also, for both species the importance of the dominant age-group in the yield is more pronounced in the age-structured version of the model. All these differences are the consequence of not taking into account the size-selective impact of fishing gear.

DISCUSSION

A size- and age-structured dynamic pool model has been developed to integrate existing knowledge on the population dynamics of pikeperch and perch in Lake IJssel. The differentiation into size categories was deliberately chosen, because interactions between gears and species are more directly related to size than to age.

The 'fractional boxcar train method', introduced to control growth dispersion within an age-group, clearly allows an evaluation of the size-selective impact of gill nets on a fish stock, which has been considered an important limitation of other existing models for gill net fisheries (Berkes and Gönenc, 1982). Calculations with other types of models, which were based on individuals ($10,000 \pm 2,000$ recruits) and characterised by specific values of L_{∞} and k taken randomly from assumed normal distributions (Hampton and Majkowski, 1987), appear to be much more time-consuming than our model (which used 8 age-groups divided over 100 size-classes).

The present version of our model has a number of limitations. First, uncertainty exists with respect to the potential growth and natural mortality of pikeperch and perch in unexploited situations. Willemsen (1983) stated that his estimate for the potential growth of pikeperch is conservative. For perch there are to date no estimates of potential growth. The opercula which were used to calculate the growth were taken from the perch population in Lake IJssel. Age 4 and 5 perch had already been exploited by the gill net fishery there, so their size distributions were probably altered by size-selective removal of the larger specimens. Although Willemsen (1977) describes faster growth of perch in Lake IJssel, which is more in line with the observed growth, we preferred to use our own data, because they contained information on sexual differences in growth rate. Estimates of natural mortality for the currently exploited age-groups are

tentative. For perch, natural mortality varied largely from year-to-year and a well-founded choice for age 3 and older could not be made (Born, 1991). Hence a constant value of $M = 0.2 \text{ yr}^{-1}$ for larger fish, as assumed in many other situations, was chosen.

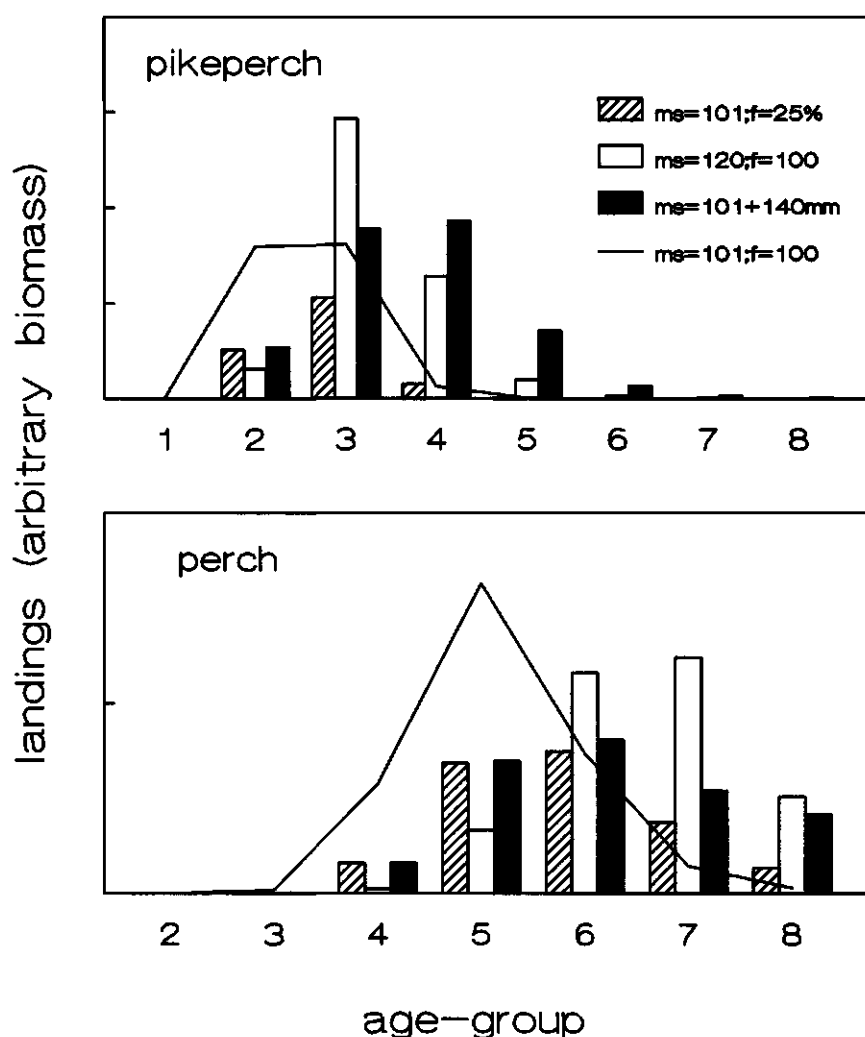


Fig. 11. Age-frequency distributions of the yield of pikeperch and perch, not accounting for size-selective processes. Line indicates the situation during the reference period; bars indicate the age composition after implementation of management measures. ms = mesh size (mm stretched mesh); f = relative fishing effort (%).

Second, it is known that some fishermen use gill nets with mesh sizes larger than the legal minimum in order to catch large pikeperch. Calculations were made under the assumption that in the case of a minimum legal mesh size, either 101 or 120 mm gill nets were used. This has probably resulted in unrealistic underestimations of the yield and a too high (spawning) stock biomass in the case of fisheries with 101 mm gill nets only.

Third, the model is density-independent and therefore acts just as a refined Beverton and Holt yield-per-recruit model. Up to now, stock-recruitment relationships have not been quantified, but inter- and intra-specific interactions in respect of recruitment might alter the results of simulations significantly. Although, the food web structure is known, estimates of energy fluxes are uncertain (Buijse et al. 1990). Once quantified, density-dependent processes will be incorporated into the model as has been done for e.g. walleye, *Stizostedion vitreum* (Jensen, 1989).

Fourth, recruitment was held constant in the present version of the model. Variation in recruitment will not influence the consequences of management measures in terms of maximum yield, as long as density-dependent processes for the two stocks are not incorporated in the model. Variation in recruitment has, however, a direct effect on the stability of the yield. Therefore management strategies should in future be evaluated on the basis of maximum yield as well as stability in the yield.

So far the model could only be validated by comparing the size and age structure of the simulated and of the observed yield and stock. Although there is a high degree of similarity, there appear to be marked differences, which might be resolved by specific data collections. In particular, discard practices appear to be an important issue.

Simulation of the different management strategies indicate that all options have a positive influence on the spawning stock size of both species, with the exception of pikeperch in the case where the legal minimum mesh size is increased to 120 mm. A substantial permanent reduction of the yield was observed only for pikeperch when the fishing effort with 101 mm gill nets is reduced by 75% and no other mesh size is allowed, because pikeperch quickly grew through the selection curve. Considering the losses during the transitional period and the gain thereafter, the combination of a reduced number of 101 mm gill nets with the addition of 140 mm gill nets, seems to be the most profitable management strategy.

Due to the model being size-structured, it appears to be very suitable for analysing the impact of gill net fisheries on the size- and age-structure of the fish stocks. Many different methods have been suggested for calculation of the gill net selectivity (Hamley, 1975). The model is readily capable of evaluating the effect of different approaches to selection curves, like unimodal curves with

constant efficiency (Holt, 1963) or bimodal curves with increasing efficiency for larger mesh sizes (Hamley and Regier, 1973).

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REFERENCES

- Anonymous, 1969-1982. Visserij, voorlichtingsblad voor de Nederlandse visserij (Fishery, information journal for the Dutch fishery). Ministry of Agriculture and Fisheries. vol. 22-35 (in Dutch).
- Berkes, F. and Gönenc, T., 1982. A mathematical model on the exploitation of northern lake whitefish with gill nets. *North Am. J. Fish. Manag.*, 2: 176-183.
- Beverton, R.J.H. and Holt, S.J., 1957. On the dynamics of exploited fish populations. *Fishery Investigations Series II, Marine fisheries*, Great Britain. Ministry of Agriculture, Fisheries and Food 19. 533 p.
- Born, A.F., 1991. Schattingen van de aantallen en de mortaliteit van baars (*Perca fluviatilis*) in het IJssel- en Markermeer in de periode 1969-1987 (Estimations of numbers and mortalities of perch (*Perca fluviatilis*) in the IJssel- and Markermeer in the period 1969-1987). Department of Fish Culture and Fisheries, Agricultural University Wageningen. M.Sc.-thesis no. 1337. 53 p. (in Dutch)
- Buijse, A.D., Eerden, M.R. van, Dekker, W. and Densen, W.L.T. van, 1991. A trophic model for IJsselmeer (The Netherlands), a shallow eutrophic lake. In: V. Christensen and D. Pauly (Editors), *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings No. 26, p. 000-000.
- Collins, J.J., 1979. Relative efficiency of multifilament and monofilament nylon gill net towards lake whitefish (*Coregonus clupeaformis*) in Lake Huron. *J. Fish. Res. Board Can.* 36: 1180-1185.
- Dekker, W., 1983. An application of the Andersen consumption model in estimating prey size preference in North Sea cod. *ICES C.M.*1983/G:63. 16 pp.
- Dekker, W., 1991. Assessment of the historical downfall of the IJsselmeer fisheries using anonymous inquiries for effort data. In: I.G. Cowx (Editor), *Catch effort sampling strategies and their application in freshwater fisheries management*. Fishing News Books, Blackwell Scientific Publications. Oxford. p. 233-240.
- Densen, W.L.T. van., 1987. Gillnet selectivity to pikeperch, *Stizostedion lucioperca* (L.), and perch, *Perca fluviatilis* L., caught mainly wedged. *Aquacult. Fish. Manag.* 18: 95-106.
- Densen, W.L.T. van, Cazemier, W.G., Dekker, W. and Oudelaar, H.G.J., 1990. Management of the fish stocks in Lake IJssel, the Netherlands. In: W.L.T. van Densen, B. Steinmetz, R.H. Hughes (Editors). *Management of freshwater fisheries*, Proceedings of a symposium organized by the European Inland

- Fisheries Advisory Commission, Göteborg, Sweden, 31 May - 3 June 1988. PUDOC, Wageningen pp. 313-327.
- Goudriaan, J. and Roermund, H.J.W. van, 1989. Modelling of ageing, development, delays and dispersion. In: R. Rabbinge, S.A. Ward and H.H. van Laar (Editors), Simulation and systems management in crop protection. Pudoc Wageningen. pp. 47-79.
- Hamley, J.M., 1975. Review of gillnet selectivity. J. Fish. Res. Board Can., 32: 1943-1969.
- Hamley, J.M. and Regier, H.A., 1973. Direct estimates of gillnet selectivity to walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can., 30: 817-830.
- Hampton, J. and Majkowski, J., 1987. A simulation model for generating catch length-frequency data. In: D. Pauly and G.R. Morgan (Editors), Length-based methods in fisheries research. ICLARM Conference Proceedings 13. ICLARM. Manila. Philippines. pp. 193-202.
- Hightower, J.E. and Grossman, G.D., 1987. Optimal policies for rehabilitation of overexploited fish stocks using a deterministic model. Can. J. Fish. Aquat. Sci. 44: 803-810.
- Hokanson, K.E.F., 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34: 1524-1550.
- Holt, S.J., 1963. A method for determining gear selectivity and its application. ICNAF Spec. Publ. 5: 106-115.
- IBM 1975. Continuous System Modeling Program III. Program reference manual SH19-7001-2. Techn. Publ. Dept., White Plains, USA.
- Jacobson, P.C. and Taylor, W.W., 1985. Simulation of harvest strategies for a fluctuating population of lake whitefish. North Am. J. Fish. Manag. 5: 537-546.
- Jensen, A.L., 1989. Simulation of the potential for life history components to regulate walleye population size. Ecol. Model. 45: 27-41.
- Le Cren, E.D., 1947. The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. J. Anim. Ecol. 16: 188-204.
- Le Cren, E.D., 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years, with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27: 287-334.
- McCombie, A.M. and Berst, A.H., 1969. Some effects of shape and structure of fish on selectivity of gillnets. J. Fish. Res. Board Can. 26: 2681-2689.
- Pet, J.S., 1988. An interactive size- and age-structured simulation model for the gillnet fishery on pikeperch and perch in Lake IJssel. M.Sc. Thesis Agricultural University Wageningen. Department of Fish Culture and Fisheries (Rep. No. 1276) and Department of Theoretical Production Ecology. 126 p.
- Peterson, I. and Wroblewski, J.S., 1984. Mortality rates of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci., 41: 1117-1120
- Pitcher, T.J. and Hart, P.J.B., 1982. Fisheries ecology. Croom Helm, London. 414 pp.
- Ricker, W.E., 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.

- Schaap, L.A., 1987. Vergelijking van de vangsten in mono- en multifilament staande netten in het IJsselmeer (comparison of catches in mono- and multifilament gill nets in Lake IJssel). Netherlands Institute for Fishery Research. IJmuiden. Report BV 87-03. 12 p. (in Dutch).
- Silvestre, G.T. and Soriano, M.L., 1988. Effect of incorporating sigmoid selection on optimum mesh size estimation for the Samar Sea multispecies trawl fishery. In: S. Venema, J. Möller-Christensen and D. Pauly (Editors), Contributions to tropical fisheries biology: Papers presented by the participants of FAO/DANIDA Follow-up training courses. FAO Fish. Rep. No. 389. pp. 482-492.
- Sissenwine, M.P., 1977. A compartmentalized simulation model of the southern New England yellowtail flounder, *Limanda ferruginea*, fishery. Fish. Bull., 75: 465-482.
- Staub, E., Büttiker, B. and Krämer, A., 1987. Grundlagen für Modellsimulationen zur Bewirtschaftung des Barsches (*Perca fluviatilis* L.) im Bodensee. Bundesamt für Umweltschutz, Bern. Schriftenreihe Fisherei. Nr. 46. 40 p.
- Thorpe, J.E., 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. J. Fish. Res. Board Can. 34: 1504-1514.
- Willemsen, J., 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34: 1710-1719.
- Willemsen, J., 1978. Influence of temperature on feeding, growth and mortality of pikeperch and perch. Verh. Internat. Verein. Limnol. 20: 2127-2133.
- Willemsen, J., 1983. Biology and management of pikeperch. Proc. 3rd. Brit. Fresw. Fish. Conf. p. 115-125.
- Wit, C.T. de, 1982. Coordination of models. In: F.W.T. Penning de Vries and H.H. van Laar (Editors), Simulation of plant growth and crop production. Pudoc, Wageningen. pp. 26-31.
- Wit, C.T. de and Goudriaan, J., 1978. Simulation of ecological processes. Pudoc, Wageningen. 175 p.

Chapter 7

RECRUITMENT-INDUCED VARIATIONS OF THE YIELD AND THE CONSEQUENCES FOR THE MANAGEMENT OF THE GILL NET FISHERY ON PERCH AND PIKEPERCH IN LAKE IJssel.

Catches of pikeperch and to a lesser extent perch in Lake IJssel vary greatly from year to year. This chapter combines the observed variation in recruitment (Chapter 3) with the size- and age-structured simulation model (Chapter 6) to demonstrate the possibilities to stabilise the yield to a certain level. A model, which relates the variation in the yield to variations in recruitment, demonstrates that the stabilisation of the yield depends on the age composition of the catches. The results are discussed in relation to the uncertainty in the yield prediction, based on young-fish surveys. It is concluded that effects of altered management will be difficult to demonstrate, if the increase in yield merely consists of a higher yield per recruit.

INTRODUCTION

This final chapter deals with the perspectives for stabilising the yield of percids from the gill net fishery in Lake IJssel. Successful exploitation of a fishery depends not only on the quantity of fish caught, but also on the steadiness of the supply (MacLennan and Shepherd 1988; Silvert 1982). The advantages of a stable yield are obvious with respect to marketing, a stable income and besides, effects of management measures are more lucid. The variation in the yield increases with increasing effort especially when maximum sustainable yield levels are exceeded (Beddington and May 1977; May et al. 1978).

Annual variation in the yield in intensively exploited fish stocks is mainly caused by variation in recruitment. Comparison of recruitment estimates and associated catches over time in a large number of marine fish stocks indicated that significant deviations in catch closely followed significant deviations in recruitment (Hennemuth et al. 1980). The variation in the yield of the commercial gill net fishery in Lake IJssel for pikeperch (*Stizostedion lucioperca*) and perch (*Perca fluviatilis*) is high (Fig. 1; Van Densen et al. 1990). Over the period 1947-1987 the long-term coefficient of variation (CV) was 95% and 76% while the year-to-year variation (the ratio between the mean of the absolute difference between two consecutive years and the mean long-term annual yield) was 65% and 27% for pikeperch and perch respectively, which was considered high for pikeperch and moderate for perch when compared with 121 exploited fish stocks (mean long-term CV = 63%, mean year-to-year variation = 34%) (Buijse et al. 1991). The large variation of pikeperch especially is among others due to variation in recruitment in combination with a high exploitation rate (Van Densen et al. 1990; Willemsen

1977). Recruitment of pikeperch varied 70-fold and of perch 400-fold in Lake IJssel over the period 1966-1989 (Fig. 2).

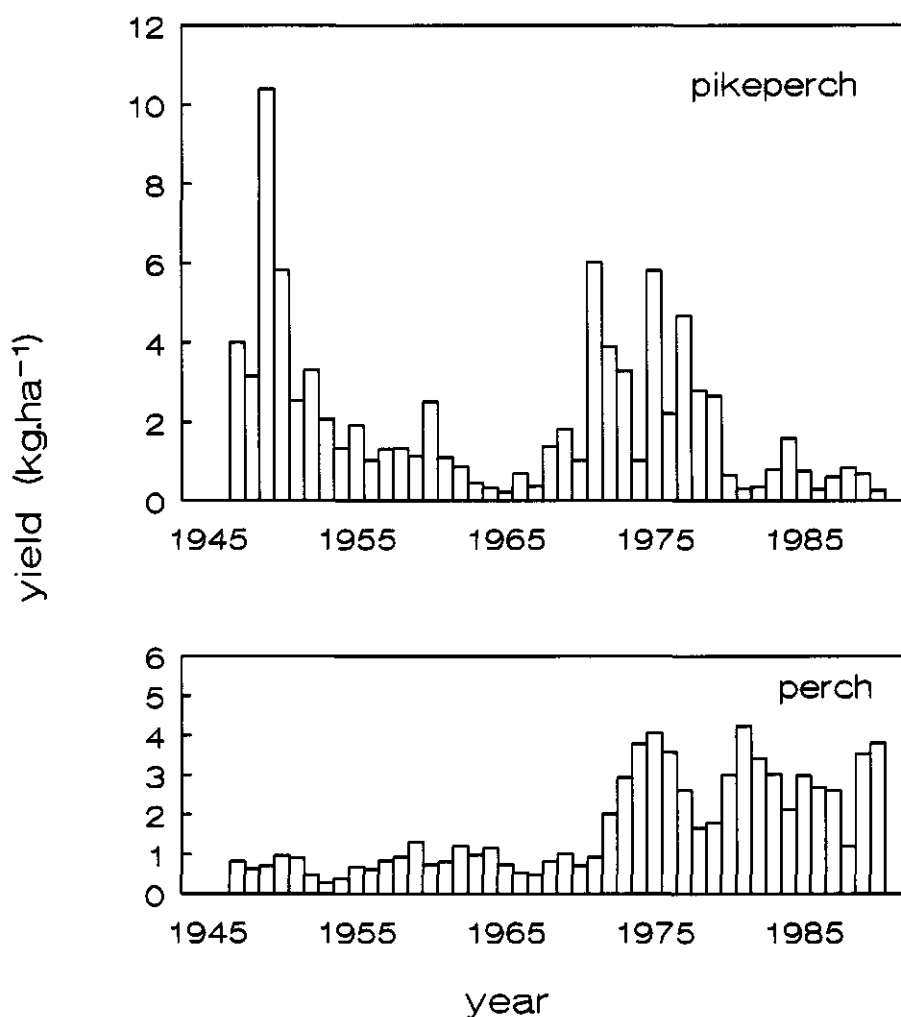


Fig. 1 Annual yield of pikeperch and perch in Lake IJssel over the period 1947-1987.

A constant quota policy could stabilise this variation in the yield, but is regarded to be less profitable than a constant effort policy (Jacobson and Taylor 1985). In a simulation of the Pacific whiting (*Merluccius productus*) fishery, Swartman et al. (1983) have shown that constant quota would have decimated the stock after a number of consecutive unfavourable (cold) years, whereas this

would not happen in case of a constant effort policy or stock protection policy. Consequently, constant quota policy must be more conservative in the exploitation rate than the other policies mentioned. Managing fisheries with a constant effort policy will result in variation of catches. Fisheries managers must then be prepared to make a trade-off between maximisation of the yield and minimisation of the variance of the yield (May et al. 1978; Silvert 1982).

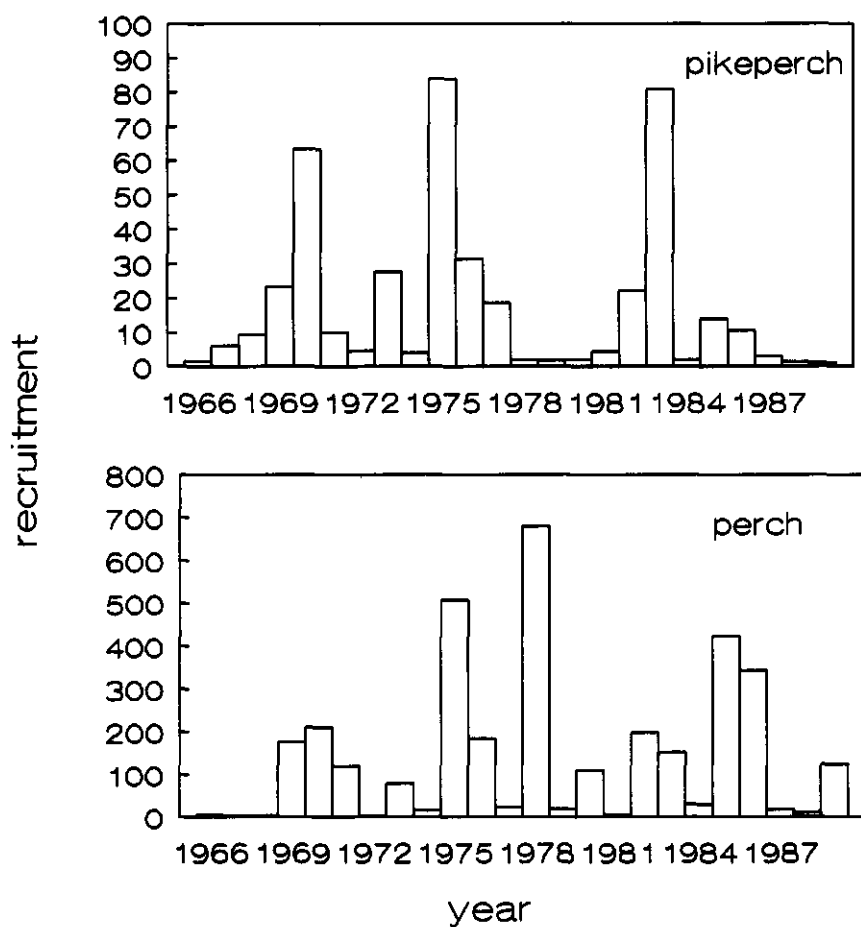


Fig. 2 Year-class strength variation of pikeperch and perch, indexed as the number of age 0 fish per standard bottom trawl haul of 10 min, in Lake IJssel over the period 1966 - 1989. Data on age 0 abundance from the northern and southern part were averaged (Buijse et al. 000).

Until 1991 the gill net fishery for perch and pikeperch in Lake IJssel has been regulated by minimum mesh sizes and by effort limitation via closed periods only. The number of gill nets have increased continuously since the early 1970s (Dekker 1991; Van Densen et al. 1990). However, since 1991 every fishing company was assigned a fixed number of gill nets, and the fishery can now be regarded to be managed with a constant effort policy.

In this chapter the stock dynamics and the exploitation of pikeperch and perch is simplified by regarding variations in year-class strength (YCS) as a fait accompli and by managing the fishery with a constant effort policy. Neither for pikeperch nor for perch recruitment could be shown to depend on stock size (Buijse et al. 000). Since modelling results depend critically on any stock-recruitment relationship imposed on the stock (May et al. 1978), it seems appropriate to neglect the possible dependence of recruitment on stock size, when investigating the possibilities to stabilise the yield.

A size- and age-structured simulation model has been developed for evaluating management measures for gill net fisheries (Buijse et al. 1992). The output of the model consists among others of the relative contribution by weight of every age-group to the yield. Buijse et al. (1992) have evaluated several management measures for maximising the yield per recruit of pikeperch and perch in Lake IJssel. In this chapter the same management measures are evaluated for their potential to stabilise the yield. This chapter focuses on the feasibility to stabilise the variable yield of pikeperch and perch in Lake IJssel. It deals with the consequences of variation in YCS and of other sources of uncertainty for the reliability of the predicted change in yield following changes in management.

The model

The following model illustrates that under a constant effort policy the possibilities to stabilise the yield depend on the initial variation in YCS and the exploitation pattern of the stock. It is assumed that variation in YCS is the most important source of variation in the yield. Other sources of variability, e.g. variations in growth and vulnerability to fishing gear, were at this stage ignored. The model corresponds largely to a model recently developed to evaluate effects of fishing effort on the variation in catches of marine fish (MacLennan and Shepherd 1988).

The annual yield per age-group (Y_i in kg) is determined by its recruitment at age 0, the total mortality up to the year in question, the exploitation rate and the mean weight per fish.

$$Y_i = R_{j-i} * e^{-\sum_{n=1}^i Z_{n-1}} * (1 - e^{-Z_i}) * \frac{F_i}{Z_i} * W_i \quad (1)$$

where:

F = instantaneous fishing mortality rate (yr⁻¹)

i = age-group

j = year (here year of birth)

n = integer

R = number of recruits at age 0

W = mean weight of fish with age i (kg)

Z = instantaneous total mortality rate (yr⁻¹)

The total annual yield (Y in kg) is a summation of the yield per age-group

$$Y = \sum_{i=a}^A Y_i \quad (2)$$

where:

a = youngest age-group in the yield

A = oldest age-group in the yield

In case of a constant fishing and natural mortality for each particular age-group ($F_{i,j} = F_{i,j+1}$, and $M_{i,j} = M_{i,j+1}$), but allowing for variations with age, the coefficient of variation (CV) of the yield of an age-group over a series of years equals the coefficient of variation of the number of recruits.

$$CV_{Y_i} = CV_R \quad (3)$$

The variance of a sum of several age-groups is (Sokal and Rohlf 1981 p. 573)

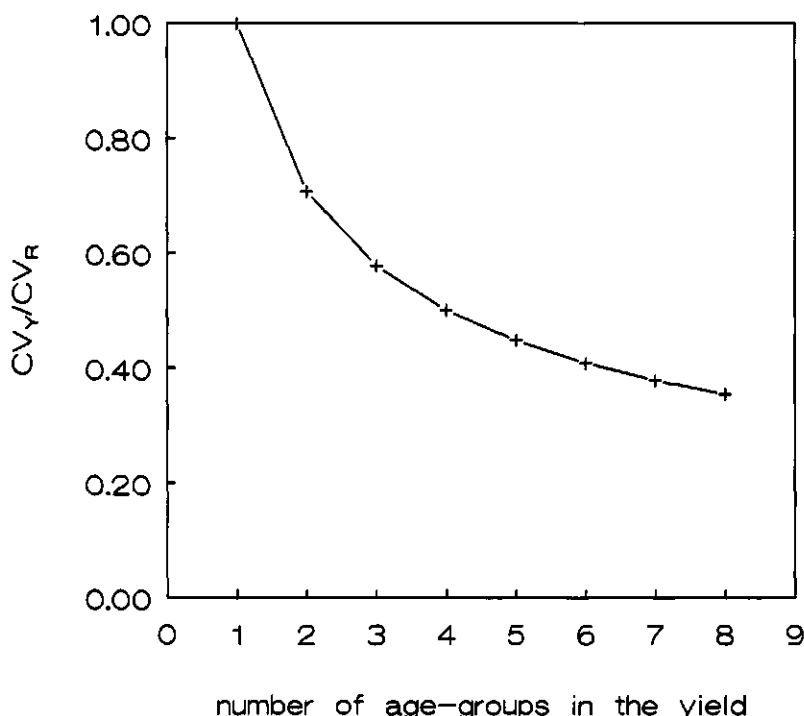


Fig. 3 Yield stabilisation ($CV_Y:CV_R$ ratio) as function of the number of age-groups in the yield. In this theoretical example each age-group has the same relative contribution i.e. if the yield comprises four age-groups then every age-group contributes 25% of yield by weight. CV_Y = coefficient of variation in the yield; CV_R = coefficient of variation in recruitment.

$$SD_Y^2 = \sum_{i=1}^A SD_{Y_i}^2 + \sum_{i=1}^A \sum_{n=1}^{A-i} 2 * r_{i, i+n} * SD_{Y_i} * SD_{Y_{i+n}} \quad (4)$$

where:

SD = standard deviation of the yield

$r_{i, i+n}$ = correlation coefficient between the yield of two age-groups i.e. the serial coefficient of correlation between recruitment indices with various time-lags

The standard deviation of the annual yield per age-group equals the coefficient of variation multiplied by the mean, which combined with eq. 3 results in:

$$SD_{Y_i} \approx \bar{Y}_i * CV_R \quad (5)$$

Combining eq. 4 and 5 results in:

$$SD_Y^2 = CV_R^2 \left(\sum_{i=a}^A \bar{Y}_i^2 + \sum_{i=a}^A \sum_{n=1}^{A-i} 2 * r_{i,i+n} * \bar{Y}_i * \bar{Y}_{i+n} \right) \quad (6)$$

Thus the variation in the total annual yield is estimated by eq. 7.

$$CV_Y = CV_R * \sqrt{\frac{\sum_{i=a}^A \bar{Y}_i^2 + \sum_{i=a}^A \sum_{n=1}^{A-i} 2 * r_{i,i+n} * \bar{Y}_i * \bar{Y}_{i+n}}{Y}} \quad (7)$$

Eq. 7 states that the variation in the yield is a function of variation in recruitment (first part), and a function of the number and relative contribution of age-groups in the yield and the serial correlations between recruitment indices with various time-lags (second part). The yield is more stabilised if it comprises more age-groups and if it is more evenly distributed by weight among the age-groups. It also demonstrates that the variation in the yield will increase when recruitment is positively correlated ($r_{i,i+n} > 0$) with that in previous years, and decrease when negatively correlated ($r_{i,i+n} < 0$).

If serial correlation analysis of recruitment data indicate that recruitment in one year is not significantly correlated with that in previous years then $r_{i,i+n}$ is assumed to be zero and the variation in the total yield can be simplified to eq. 8.

$$CV_Y = CV_R * \sqrt{\frac{\sum_{i=a}^A \bar{Y}_i^2}{Y}} \quad (8)$$

To illustrate the stabilising effect of an increased number of age-groups on the variation in the yield a simple theoretical exploitation of a stock is presented: serial coefficients of correlation are zero, and the exploitation rate

is such that every age-group has the same relative contribution by weight to the yield. The $CV_Y:CV_R$ ratio is then equal to the square root of the inverse of the number of age-groups in the yield. If, under such circumstances, the yield comprises only one age-group as in case of extremely high fishing intensity, then the variation in the yield would equal the variation in recruitment. On the other hand, if the yield comprises e.g. eight age-groups then the relative contribution per age-group would be 0.125, and the variation would have been damped to 0.35 ($=\sqrt{0.125}$) of the initial variation in recruitment (Fig. 3). Fig. 3 illustrates that the gain of increasing the number of age-groups in the yield via management measures in damping variation is initially large, but decreases quickly when in the initial situation the yield already consisted of several age-groups.

The gill net fishery on percids in Lake IJssel

Although age 0 abundance and future landings of pikeperch and perch are significantly correlated, management still has to deal with large confidence limits around the predicted yield. Both for pikeperch and perch accumulated landings per year-class in the gill net fishery were significantly correlated with their abundance as age 0 in survey trawls (Buijse et al. 000). So based on young fish surveys future yield might be predicted (Fig. 4). It is obvious that the predicted yield is still highly uncertain with the knowledge of the YCS as age 0 fish: predicting the yield of an individual year-class is virtually impossible, because lower and upper 95% confidence limits differ at least 12.1-fold for pikeperch and 6.4-fold for perch; predicting the mean yield over a numbers of years given a certain YCS results for pikeperch in confidence limits which differ at least 1.6-fold, and for perch 2.7-fold.

Simple calculations showed that serial correlation coefficients between recruitment estimates with a 1-yr to 5-yr lag were not significant (Table 1). The stabilisation of the yield as a consequence of various management measures was consequently calculated according to eq. 8.

Table 1. Serial correlation analyses of the recruitment data in 1 year with that of the previous 1 to 5 years. Analysis are based on data on age 0 fish abundance in Lake IJssel in November. Data from the northern and southern part were averaged (Buijse et al. 000).

| | n | 1-yr lag | 2-yr-lag | 3-yr lag | 4-yr lag | 5-yr lag |
|-----------|----|----------|----------|----------|----------|----------|
| perch | 24 | 0.032 | -0.024 | -0.273 | -0.041 | 0.165 |
| pikeperch | 24 | 0.250 | 0.004 | -0.261 | -0.352 | -0.125 |

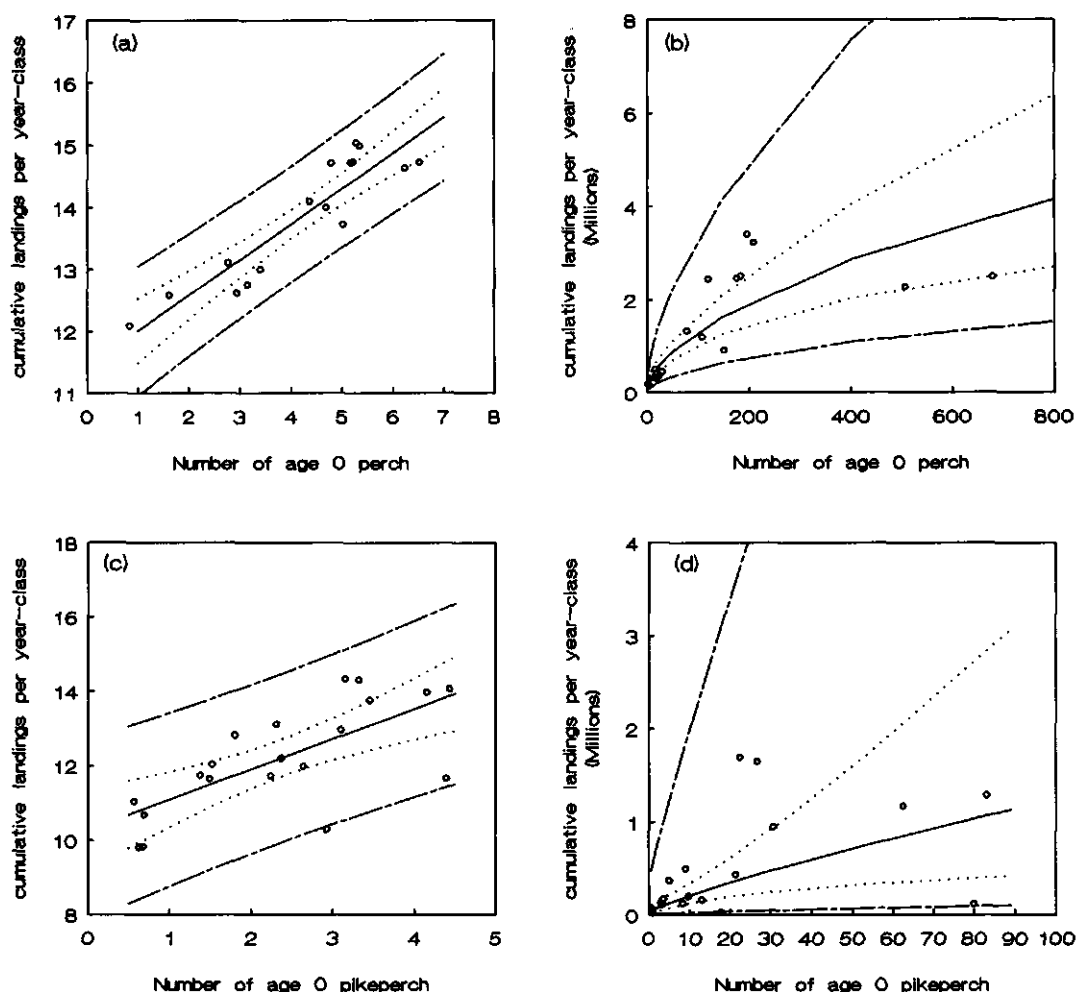


Fig. 4 Accumulated landings per year-class versus their age 0 abundance in survey trawl catches in November (no.(10 min trawling)⁻¹) (Buijse et al. 000). (a) and (b) log_e-transformed and untransformed data for perch; (c) and (d) log_e-transformed and untransformed data for pikeperch; fitted (.....) and predicted (— · — ·) 95% confidence interval of the mean.

The model developed by Buijse et al. (1992) estimates the relative contribution by weight of various age-groups given a certain management measure. With these results it is possible to estimate the stabilising effect of a management measure on the yield. In Buijse et al. (1992) the effect of five management measures were evaluated. The relative contribution of age 2 to 7

fish and the resulting $CV_Y:CV_R$ ratio as calculated with eq. 8 are listed in Table 2. The $CV_Y:CV_R$ ratio based on the simulation of the initial situation was 0.64 for pikeperch and 0.58 for perch. Based on the commercial landings and the recruitment index found with the young fish trawl survey the $CV_Y:CV_R$ ratio was 0.73 (yield over the period 1968-1990; recruitment 1966-1988) for pikeperch, which was somewhat higher than in the simulation, while for perch it was 0.33 (yield 1970-1990; recruitment 1966-1986), which is much lower than in the simulation.

The graphic comparison between the simulated and the observed yield in the initial situation shows that for pikeperch the variations were in the same order of magnitude, while for perch the variations in the simulated yield were stronger than in the observed yield (Fig. 5). The variation in the annual simulated landings was estimated by combining the observed variation in YCS (Fig. 2) with the relative contribution of the various age-groups to the total annual yield in the initial situation before any management measure is taken (Table 2). For pikeperch, increases in the simulated yield appeared later than in the observed yield. This might point towards a larger contribution of age 1 and 2 fish to the yield than simulated, because the time-lag between a strong year-class and an increase in yield is shorter. The discrepancy between simulated and observed yield of pikeperch in the mid 1980s is due to the unexpected low landings of the very strong year-class 1983 (Fig. 2).

The simulated yield in the initial situation was compared with the simulated yield for the management situations mentioned in Table 2 to evaluate the effects of those measures on the variation in the yield (Fig. 6). The predicted change in mean yield (Table 2) is also accounted for in the calculation of the yields. Conclusions with regard to the predicted change in mean yield and the age-composition of the yield were discussed by Buijse et al. (1992). It is clear, that irrespective of management measure there will always be a large variation in the yield as a consequence of the variations in recruitment. A combination of two mesh sizes, whereby the number of 101 mm gill nets are reduced by 75% and a number of 140 mm gill nets without a reduction in effort (i.e. the same effort as with 101 mm gill nets in the initial situation) had the largest stabilising effect on the yield. Even in that case the effect is rather limited. For perch the $CV_Y:CV_R$ ratio is expected to decrease from 0.58 to 0.54 and for pikeperch from 0.64 to 0.54.

Table 2. Relative contribution of age 2 to 7 pikeperch and perch to the yield under various management measure (Buijse et al. 1992). MS = mesh size; f = effort; Y = predicted change in yield are percentage of the initial Y for each species separately; CV_Y:CV_R ratio was calculated according to eq. 8 (see text).

| Management measure | MS (mm) | f (%) | Open season | Y | age-group | | | 5 | 6 | 7 | CV _Y :CV _R ratio |
|--------------------|---------|-------|--------------------|-----|-----------|------|------|------|------|------|--|
| | | | | | 2 | 3 | 4 | | | | |
| Pikeperch | | | | | | | | | | | |
| Initial situation | 101 | 100 | 1 July-15 March | 100 | 0.36 | 0.52 | 0.11 | 0.01 | 0.00 | 0.00 | 0.64 |
| 1 | 120 | 100 | 1 July-15 March | 132 | 0.06 | 0.51 | 0.35 | 0.07 | 0.01 | 0.00 | 0.62 |
| 2 | 101 | 25 | 1 July-15 March | 61 | 0.19 | 0.51 | 0.25 | 0.05 | 0.00 | 0.00 | 0.60 |
| 3 | 101 | 100 | 1 October-15 March | 96 | 0.30 | 0.52 | 0.16 | 0.02 | 0.00 | 0.00 | 0.62 |
| 4 | 101 | 25 | 1 July-15 March | 134 | 0.09 | 0.35 | 0.37 | 0.16 | 0.03 | 0.00 | 0.54 |
| [| | | | | | | | | | | |
| Perch | | | | | | | | | | | |
| Initial situation | 101 | 100 | 1 July-15 March | 100 | 0.00 | 0.05 | 0.42 | 0.37 | 0.13 | 0.03 | 0.58 |
| 1 | 120 | 100 | 1 July-15 March | 119 | 0.00 | 0.00 | 0.06 | 0.34 | 0.39 | 0.21 | 0.56 |
| 2 | 101 | 25 | 1 July-15 March | 110 | 0.00 | 0.02 | 0.24 | 0.40 | 0.25 | 0.09 | 0.54 |
| 3 | 101 | 100 | 1 October-15 March | 105 | 0.00 | 0.05 | 0.38 | 0.39 | 0.15 | 0.04 | 0.56 |
| 4 | 101 | 25 | 1 July-15 March | 110 | 0.00 | 0.02 | 0.24 | 0.40 | 0.25 | 0.10 | 0.54 |
| [| | | | | | | | | | | |

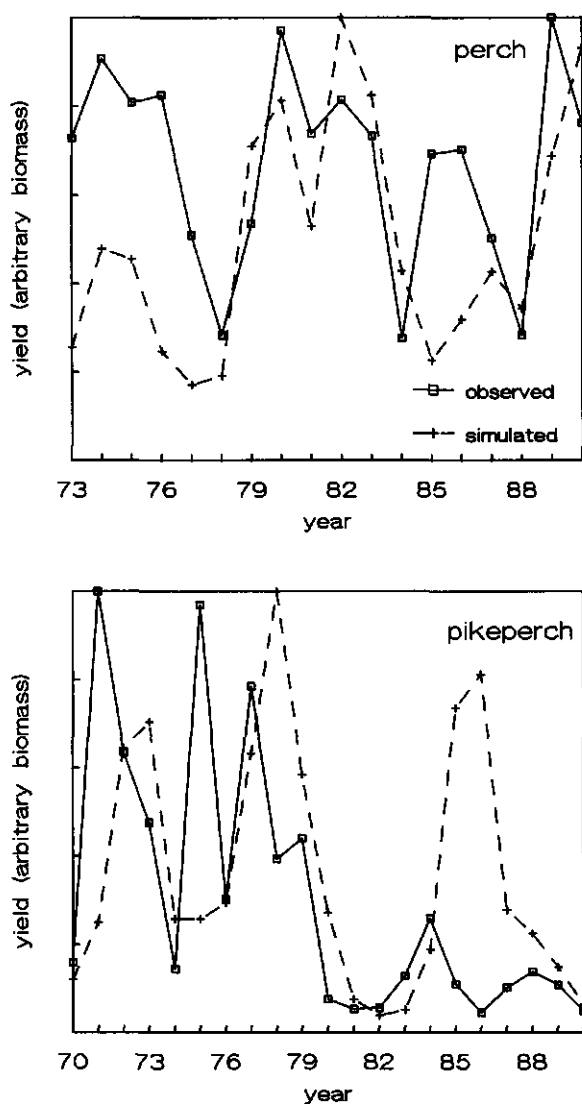


Fig. 5 Observed and simulated annual yield of perch and pikeperch. Observed annual yields were calculated from 1 April to 31 March in the following year. Simulated yields are based on their age 0 abundance in survey trawl catches (no.(10 min trawling)⁻¹) over the period 1966-1988 (Buijse et al. 000) and the estimated exploitation pattern over the period 1974-1983 (Buijse et al. 1992).

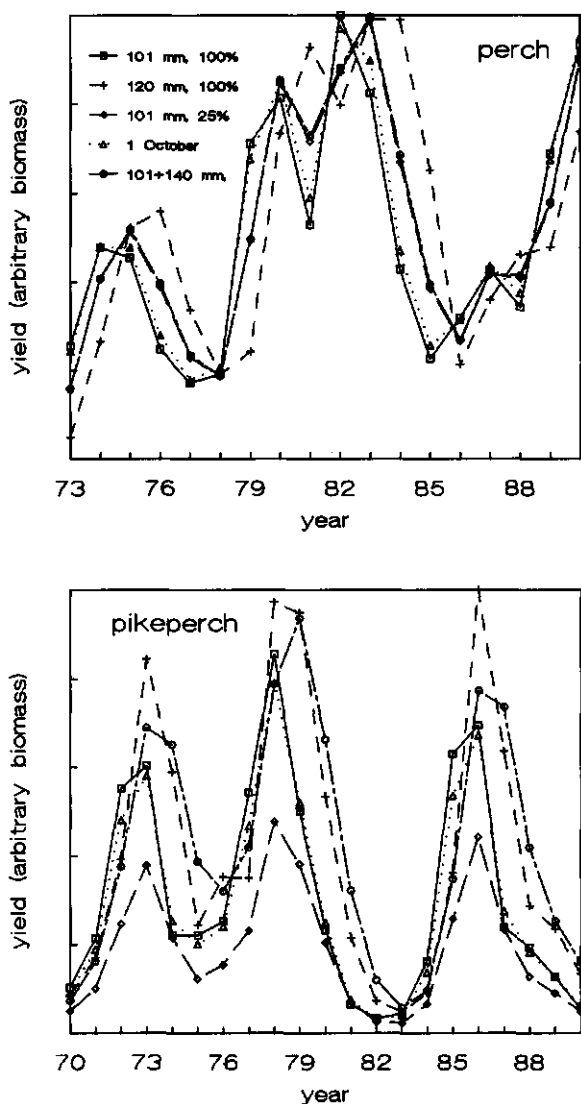


Fig. 6 Theoretical yield of perch and pikeperch in case the gill net fishery would have been managed otherwise. Estimates of the annual yield, given a certain management, are based on the age 0 fish abundance in survey trawl catches (no.(10 min trawling)⁻¹) in November over the period 1966-1988 (Buijse et al. 000), and the change in mean yield and the age composition of the yield (Table 2). 101 mm, 100%: exploitation pattern over the period 1974-1983 with a gill net mesh size = 101 mm stretched mesh and an effort of 100%; 120 mm, 100%: mesh size is enlarged to 120 mm; 101 mm, 25%: effort is reduced to 25%; 1 October: the closed season is extended from 1 July to 1 October; 101+140 mm: effort with 101 mm gill nets is reduced to 25% and 140 mm gill nets are used with an effort of 100%.

DISCUSSION

Knowing that variations in recruitment are one of the most important factors causing stocks and yield to vary, possibilities to stabilise the yield should be evaluated in the light of recruitment variations. A simple model was used to relate the variation in the yield to variations in recruitment and the exploitation pattern. The $CV_Y:CV_R$ ratio supplies general information on the exploitation rate of a fish stock. The model demonstrated that the effect of stabilisation due to a lower fishing effort is higher in case a stock is more intensively exploited i.e. when the yield comprises less age-groups. This agrees with models of e.g. Beddington and May (1977) and May et al. (1978), who demonstrated that the variation will increase especially at higher levels of fishing effort when maximum sustainable yield levels are exceeded.

Certainly, the dynamics and exploitation of the percid stocks are simplified by this approach. Some density-dependent processes do probably operate even if it has not yet been possible to quantify them and fishing effort is probably not entirely constant, because fishermen may shift to other resources when catches are low. Notwithstanding, the model clarified that the possibilities for stabilizing yield by management with a constant effort policy is rather limited. Also MacLennan and Shepherd (1988), who evaluated the possibilities to stabilise the catches of cod and haddock with a constant effort policy, concluded that the benefit to be expected from any practicable decrease of F is marginal. These results seems to fit a quotation of Dickie (1979) "the mystique of conservation which has surrounded management, may have led us to expect regulation to play an unrealistically important role in stabilising yields".

The results of the simulation model did not entirely match the observed landings of pikeperch and perch. The differences may have been caused by a variety of factors e.g. increased effort over the period investigated (Dekker 1991), increased mortality of juvenile percids due to the fyke net fishery for eel (Willemsen 1985) and to bird predation (Buijse et al. 1991) or annual variations in water temperature. For pikeperch the modelled $CV_Y:CV_R$ ratio did not differ much from the observed $CV_Y:CV_R$ ratio. The faster increase of the observed yield than of the simulated yield after the recruitment of a strong year-class might be a systematic difference, indicating that the exploitation of age 2 is even stronger than simulated. The difference may also partly be caused by not taking into account year-to-year variations in temperature. Warm summers generally result in faster growth and strong year-classes, which might result in an earlier recruitment to the fishery of strong year-classes especially. In some years already age 1 fish are caught (Buijse et al. 000, Appendix 2), while the model was based on a constant age at recruitment.

For perch the observed ratio between the CV_y and CV_t was much lower than simulated. Based on the ratio of 0.33 the yield should have comprised at least 9 age-groups (if every age-group has the same relative contribution to the yield), which is not observed in market samples where hardly any fish of age 8 and older is observed (Buijse et al. 000, Appendix 1). Compensatory density-dependent mortality might have acted upon the younger unexploited age-groups of perch. E.g. density-dependent growth of strong year-classes (Buijse and Van Densen 000), might result in a prolonged period with natural mortality reducing numbers until these year-classes recruit to the fishery.

Even though observed and simulated yield did not coincide fully, the conclusions from the model are still thought to be valid: there are only limited possibilities to stabilise the yield with constant effort policy.

Due to the large variations in recruitment, and uncertainties in predicting future yields on the basis of young fish surveys, it will prove very difficult to show convincingly ultimate profits resulting from changes in management. Management has to deal with two types of uncertainty: natural and scientific. Natural fluctuations affect the dynamics and abundance of fish stocks in an unpredictable way, while scientific uncertainty is caused by the limitations that accompany attempts to monitor abundance of stocks and to explain the causal mechanisms underlying their dynamics (Beddington et al. 1984). Scientific uncertainty in case of Lake IJssel can perhaps best be illustrated by the way recruitment indices were determined, which was a young fish trawl survey comprising between four and 13 trawl hauls of 10-45 min annually. These surveys therefore covered 0.8 to 3.6 ha out of a total lake area of 182,000 ha. It is not exactly known what the confidence limits around these recruitment indices are, but they cannot be expected to be very precise.

Managers and fishermen will have to be convinced on a theoretical basis by scientists that, given the present knowledge of growth and mortality rates, altered management for the Lake IJssel fishery should result in a yield increase. Caddy and Gulland (1983) divided fish stocks into four classes according to their overall patterns of persistence: steady, cyclical, irregular and spasmodic. The pattern of the stocks of perch and pikeperch in Lake IJssel can be classified as irregular: catches vary greatly from year to year without any clear pattern. A common reason for such situations is that recruitment is highly variable, with no obvious relation to the abundance of the spawning stock. For such stocks the objective would presumably be to optimise the yield per recruit, perhaps with an overriding constraint that the spawning stock should not be allowed to fall below a level at which there is a risk for a fall in average recruitment. In a number of situations good management might easily lead to 20% higher catches in any one year. However, such a difference may be small compared with some of the year-to-year changes, which will mask the positive effect (Caddy and

Gulland 1983). This does not mean that management has little value, but stresses the fact that the value is difficult to demonstrate.

The increase in yield per recruit estimated might be regarded as a pessimistic prediction of yield increase following altered management (Buijse et al. 1992). Buijse et al. (000) and Willemsen (1983) have suggested that the pikeperch stock in Lake IJssel is recruitment over-fished, but variable mortality during the first summer has obscured the validation of this statement so far. Perhaps bold management experiments are necessary to indicate the possibilities to increase stock and yield, as suggested by Walters and Collie (1988) and Walters and Holling (1990). Lake IJssel offers unique possibilities in this context, because it is separated into a northern and southern part. At present catches in the southern part are low and of minor importance for the total revenues. The southern part appears to provide an almost ideal starting point for a large scale management experiment by drastically reducing the fishing effort for e.g. a five-years period and evaluate the development of the fish stocks. Unfortunately, such adaptive management is often hampered by a large body of dependent users, which prefer a status quo even when they are aware that altered management will almost certainly result in higher yields. However, both managers and fishermen should realise that management decisions are made in the process of learning and that learning is the key to dealing with uncertain states of nature (Hilborn 1987).

REFERENCES

- Beddington, J.R., W.E. Armtz, R.S. Bailey, G.D. Brewer, M.H. Glantz, A.J.Y. Laurec, R.M. May, W.P. Nellen, V.S. Smetacek, F.R.M. Thuro, J.-P. Troadec, and C.J. Walters. 1984. p. 227-244. Management under uncertainty. Group report. In R.M. May [ed.] Exploitation of marine communities. Dahlem Konferenzen. Life Sciences Res. Rep. 32. Springer-Verlag. Berlin.
- Beddington, J.R., and R.M. May. 1977. Harvesting natural populations in a randomly fluctuating environment. *Science* 197: 463-465
- Buijse, A.D., and W.L.T. van Densen. 000. Flexibility in the onset of piscivory and growth depensation in Eurasian perch, *Perca fluviatilis* L.. (chapter 5)
- Buijse, A.D., W.L.T. van Densen, and M.A.M. Machiels. 1991. Characteristics in the inter-annual variation of the yield from the professional fishery in freshwater bodies of the temperate and the tropical zone. p. 305-322. In I.G. Cowx [ed.] Catch effort sampling strategies and their application in freshwater fisheries management. Fishing News Books, Blackwell Scientific Publications. Oxford.
- Buijse, A.D., W.L.T. van Densen, and L.A. Schaap. 000. Year-class strength of perch, *Perca fluviatilis* L., and pikeperch, *Stizostedion lucioperca* (L.), in relation to stock size, water temperature and wind in Lake IJssel, The Netherlands, 1966-1989. (chapter 3)
- Buijse, A.D., M.R. van Eerden, W. Dekker, and W.L.T. van Densen. 1991. A trophic model for IJsselmeer (The Netherlands), a shallow eutrophic lake. In Christensen, V., and D. Pauly [eds.] Trophic models of aquatic ecosystems. ICLARM Conference Proceedings No. 26: 000-000.

- Buijse, A.D., J.S. Pet, W.L.T. van Densen, M.A.M. Machiels, and R. Rabbinge. 1992. A size-and age-structured simulation model for evaluating management strategies in a multispecies gill net fishery. *Fish. Res.* 13: 95-117.
- Caddy, J.F., and J.A. Gulland. 1983. Historical patterns of fish stocks. *Marine Policy* 7: 267-278.
- Dekker, W. 1991. Assessment of the historical downfall of the IJsselmeer fisheries using anonymous inquiries for effort data. p. 233-240. *In* I.G. Cowx [ed.] *Catch effort sampling strategies and their application in freshwater fisheries management*. Fishing News Books, Blackwell Scientific Publications. Oxford.
- Densen, W.L.T. van, W.G. Cazemier, W. Dekker, and H.G.J. Oudelaar. 1990. Management of the fish stocks in Lake IJssel, the Netherlands. p. 313-327. *In* W.L.T. van Densen, B. Steinmetz, R.H. Hughes [eds.] *Management of freshwater fisheries, Proceedings of a symposium organized by the European Inland Fisheries Advisory Commission, Göteborg, Sweden, 31 May - 3 June 1988*. PUDOC, Wageningen.
- Dickie, L.M. 1979. Perspectives on fisheries biology and implications for management. *J. Fish. Res. Board Can.* 36: 838-844.
- Hennemuth, R.C., J.E. Palmer, and B.E. Brown. 1980. A statistical description of recruitment in eighteen selected fish stocks. *J. Northw. Atl. Fish. Sci.* 1: 101-111.
- Hilborn, R. 1987. Living with uncertainty in resource management. *N. Am. J. Fish. Manage.* 7: 1-5.
- Jacobson, P.C., and W.W. Taylor. 1985. Simulation of harvest strategies for a fluctuating population of lake whitefish. *N. Am. J. Fish. Manage.* 5: 537-546.
- MacLennan, D.N., and J.G. Shepherd. 1988. Fishing effort, mortality and the variation of catches. ICES CM 1988/G:63. 12 p. + Figures. (mimeo)
- May, R.B., J.R. Beddington, J.W. Horwood, and J.G. Shepherd. 1978. Exploiting natural populations in an uncertain world. *Math. Biosciences* 42: 219-252.
- Silver, W. 1982. Optimal utilization of a variable fish supply. *Can. J. Fish. Aquat. Sci.* 39: 462-468.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry*. W.H. Freeman and Company. New York. Second edition. 859 p.
- Swartzman, G.L., W.M. Getz, R.C. Francis, R.T. Haar, and K. Rose. 1983. A management analysis of the Pacific whiting (*Merluccius productus*) fishery, using an age-structured stochastic recruitment model. *Can. J. Fish. Aquat. Sci.* 40: 524-539.
- Walters, C.J., and J.S. Collie. 1988. Is research on environmental factors useful to fisheries management? *Can. J. Fish. Aquat. Sci.* 45: 1848-1854.
- Walters, C.J., and C.S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71: 2060-2068.
- Willemsen, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. *J. Fish. Res. Board Can.* 34: 1710-1719.
- Willemsen, J. 1983. Biology and management of pikeperch. *Proc. 3rd. Brit. Freshw. Fish. Conf.* p. 115-125.
- Willemsen, J. 1985. De invloed van de visserij met fuiken op de snoekbaars- en baarsstand in het IJsselmeer. (The influence of the fishery with fyke nets on the pikeperch and perch in Lake IJssel). Netherlands Institute for Fishery Investigations. IJmuiden. Report 85-02. 10 p. (in dutch).

Curriculum vitae

Tom Buijse is in Rotterdam op 16 april 1962 geboren. In 1980 behaalde hij het VWO-diploma aan het Christelijk Lyceum voor Zeeland in Goes. In 1987 studeerde hij af als Ingenieur in de Landbouwwetenschappen met specialisatie biologie aan de Landbouwuniversiteit in Wageningen. De doctoraalfase bestond uit de hoofdvakken Visserijkunde, Natuurbeheer en Toxicologie en een stage voor visserijkunde. Van 1987 tot 1991 is hij als assistent-in-opleiding werkzaam geweest bij de vakgroep Visteelt en Visserij, waarvan dit proefschrift het resultaat is. Sinds begin 1992 is hij weer werkzaam bij deze vakgroep als wetenschappelijk project medewerker en bestaat zijn hoofdtak uit het begeleiden van projecten in Maleisië en Nigeria.