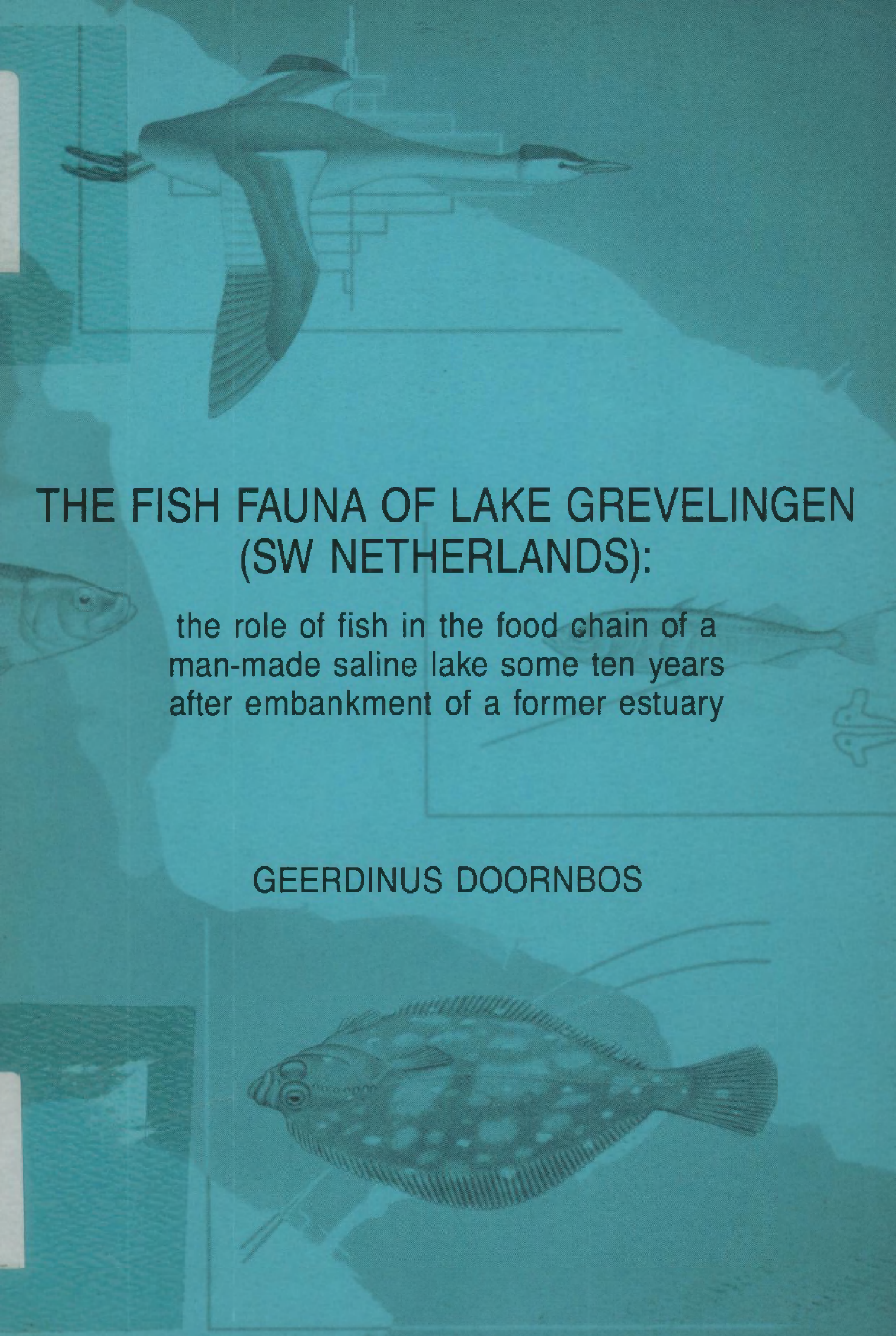


THE FISH FAUNA OF LAKE GREVELINGEN (SW NETHERLANDS):

the role of fish in the food chain of a man-made saline lake some ten years after embankment of a former estuary

GEERDINUS DOORNBOS

Omslag-ontwerp : Geerdinus Doornbos
Fred Twisk

Realisatie : Peter Twisk

26752

STELLINGEN

I

Bij het toekennen van prioriteiten binnen oecosysteem-onderzoek moet, behalve op basis van de door de verschillende plant- en diergroepen geproduceerde en/of afgebroken hoeveelheid organische stof, rekening worden gehouden met het specifieke belang van de dieren uit de hogere trophische niveaux.

II

Het onderzoek in het Deltagebied zoals dat sinds 1986 wordt uitgevoerd is ontoereikend, noch om de nog steeds optredende veranderingen in de visstand als gevolg van de waterbouwkundige werken te beschrijven, noch om op basis daarvan een adequaat beheer te baseren.

III

Introduktie van de zalm in het Grevelingenmeer verhoogt de kans dat deze vissoort weer een regelmatige gast wordt van de Nederlandse rivieren aanzienlijk.

IV

Bepalingen van diversiteitsindexen kunnen alleen het gebrek aan inzicht in oecosystemen bij de betrokken onderzoekers verbloemen.

V

In de landen van de EG dient de jachtwetgeving met betrekking tot het beheer van "trekwild" beter internationaal te worden geregeld. Het verdient aanbeveling tot een internationale quoteringsregeling te komen op basis van het broedsucces van de diverse bejaagbare soorten.

VI

Het nuttig effekt van het gebruik van het jachtgeweer ter bestrijding van wildschade wordt over het algemeen schromelijk onderschat.

VII

De gewoonte om in Zeeland slaperdijken te beheren als boom- en/of bloemdijk is in strijd met hun funktie van sekundaire waterkering.

VIII

Dat de Oosterschelde niet volledig van de Noordzee is afgesloten, maar sinds 1986 is voorzien van een stormvloedkering, is nog niet tot het Nederlands Instituut voor Onderzoek der Zee doorgedrongen.

IX

De onevenredige verschillen tussen de rechten en plichten van wetenschappelijke onderzoekers in vaste en die in tijdelijke dienst komen ondermeer tot uitdrukking in de observatie dat onderzoekers in vaste dienst mogen publiceren, terwijl tijdelijke medewerkers moeten publiceren.

X

Het in cirkulatie brengen van interne onderzoeksrapporten met indrukwekkende koderingen op de omslagen als waren het wetenschappelijk verantwoorde publikaties gaat voorbij aan de noodzakelijke kwaliteitskontrole waaraan de laatsten moeten voldoen voordat zij als basis voor beleidsbeslissingen van de Nederlandse overheid mogen dienen.

Stellingen behorende bij het proefschrift "THE FISH FAUNA OF LAKE GREVELINGEN (SW NETHERLANDS): the role of fish in the food chain of a man-made saline lake some ten years after embankment of a former estuary" van

G. Doornbos

Amsterdam, 17 juni 1987.

THE FISH FAUNA OF LAKE GREVELINGEN (SW NETHERLANDS):

the role of fish in the food chain of a man-made saline lake some ten years after embankment of a former estuary

ACADEMISCH PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR
IN DE WISKUNDE EN NATUURWETENSCHAPPEN
AAN DE UNIVERSITEIT VAN AMSTERDAM,
OP GEZAG VAN DE RECTOR MAGNIFICUS,
DR. S.K. THODEN VAN VELZEN,
HOOGLERAAR IN DE FACULTEIT DER TANDHEELKUNDE,
IN HET OPENBAAR TE VERDEDIGEN IN DE AULA
VAN DE UNIVERSITEIT (OUDE LUTHERSE KERK,
SINGEL 411, HOEK SPUI) OP WOENSDAG 17 JUNI 1987
DES NAMIDDAGS TE DRIE UUR PRECIES

door

GEERDINUS DOORNBOS

geboren te Uithuizen

Promotor : Prof. Dr. N. Daan

Co-promotor : Dr. B.R. Kuipers

Promotiecommissie: Prof. Dr. J. Ringelberg
Prof. Dr. S. van der Spoel
Prof. Dr. J.J. Zijlstra
Prof. Dr. J.W.M. Osse
Dr. J.J. Videler

During the study reported in this thesis the author was attached to the Delta Institute for Hydrobiological Research, being part of the Royal Netherlands Academy of Arts and Sciences. The study was financed predominantly by the former Environmental Division of the Delta Department (DDMI) of the Dutch Ministry of Transport and Public Works (Rijkswaterstaat).

Communication no. 365 of the Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA Yerseke, The Netherlands.

Voor Diana,
Margot en Heino

CONTENTS / INHOUD

VOORWOORD EN DANKBETUIGING

Vier jaar intensief visonderzoek, zoals in het Grevelingenmeer is verricht in het kader van het ZOWEC-projekt en dat tevens de basis vormt van dit proefschrift, betekent de samenwerking van een groot aantal personen en instanties. Zonder deze gezamenlijke krachtsinspanning was dit onderzoek minder breed en diepgaand van opzet geweest en had dit proefschrift niet gerealiseerd kunnen worden.

Mijn dank voor het bereikte eindresultaat gaat echter in de eerste plaats uit naar Fred Twisk, Roelof Bogaards en Piet de Koeijer, die zowel in het veld als op het laboratorium een onvoorstelbare hoeveelheid werk hebben verzet. Hun vakbekwaamheid, enthousiasme en uithoudingsvermogen hebben er in belangrijke mate toe bijgedragen dat de aan het begin van het onderzoek gestelde doelstellingen ook vrijwel zonder uitzondering zijn gehaald. Mede door hun hulp konden vele technische problemen, die nu eenmaal eigen zijn aan kwantitatief visonderzoek, op een adequate wijze worden opgelost. Voor hun kollegiale inzet ben ik hen zeer erkentelijk.

In de tweede plaats zou ik de bootbemanningen willen noemen: Wim Robër en Piet de Koeijer van de "Maris Stella" en Cees de Rooy en Co van Sprundel van de "Jan Verwey". Met veel genoegen denk ik nog vaak terug aan de vele vistochten die ik aan boord van de "Maris Stella" mocht meemaken. Elke tocht was weer een avontuur op zich, zowel met mooi als met slecht weer. Er werden lange dagen gemaakt. Door de korte trekduur volgden de trekken elkaar snel op en was het altijd druk aan boord. Het net moest worden geleegd en weer gereed gemaakt voor de volgende trek, de vangst moest worden gesorteerd, de grote vissen moesten worden gemeten en gewogen, terwijl de vele kleintjes (of een deel ervan) tussen de bijvangst moesten worden uitgezocht en in plastic zakken worden gedaan om op het laboratorium te worden verwerkt. Van de grote vissen moesten tevens de otolieten (gehoorsteentjes) en de magen worden uitgeprepareerd ten behoeve van de leeftijdsbepaling en het voedselonderzoek. En natuurlijk moest er een goede administratie worden bijgehouden. Het kon gebeuren dat binnen enkele uren het anders zo schone schip onder de modder, slierten zeewier, visslijm en bloedspatten zat. Zelf zat je trouwens ook al spoedig onder de smurrie en stonden je kleren en haren stijf van het zout en het visslijm. Vooral op warme dagen vermengden de geuren van dieselolie, zweet, orgaanresten, verse en minder verse vis zich met elkaar in de kleine ruimte van het laboratorium midscheeps. De geur van vers gezette koffie vanuit de stuurhut, of de aanblik van een koel flesje bier op het achterdek, vormden daarop een welkome afwisseling.

Aan Drs. Rob Lambeck, de initiatiefnemer en deelprojektleider van het ZOWEC-vissenprojekt, ben ik veel dank verschuldigd. Vanaf het begin heeft hij het onderzoek inhoudelijk van kommentaar voorzien. Daar waar artikelen (c.q. hoofdstukken) qua tekst te lang dreigden te worden heeft hij een redigerende bijdrage geleverd. Dr. Piet Nienhuis en Dr. Egbert Duursma hebben het visonderzoek steeds kritisch gevolgd en waar nodig gestimuleerd.

De voormalige Delta Dienst, Hoofdafdeling Milieu en Inrichting, van de Rijkswaterstaat (Ministerie van Verkeer en Waterstaat) heeft het grootste deel van het onderzoek gefinancierd, terwijl het Delta Instituut voor Hydrobiologisch Onderzoek voor de onderzoeksfaciliteiten (werkruimte, laboratoria, onderzoeksvaartuigen, transport, computer-gebruik, enz.) en een deel van de assistentie (Roelof Bogaards) heeft gezorgd.

Chris Almekinders en Co Hoekman hebben apparatuur voor het onderzoek gebouwd. Hulp bij het verwerken van de vele data is verkregen van Dr. Adri Vlasblom en Jan Guerand van de biomathematische afdeling van het Delta Instituut. Alfons Bolsius en Marjan van Leerdam - de Dreu hebben respektievelijk gezorgd voor de duidelijke figuren en het gave typewerk. De verschillende onderdelen van dit proefschrift zijn uiteindelijk tot één geheel samengevoegd door Jan van den Ende en Henk Kolenbrander, terwijl Peter Twisk op fraaie wijze het omslag-ontwerp gestalte heeft gegeven.

Als onderdeel van hun doktoraal-studie biologie hebben Henk Vernij, Bert Glazenburg, Vincent Erenst, Paul de Graaf en Wil Lucassen in meer of mindere mate zelfstandig meegedraaid in het visprogramma. Hun onderzoeksresultaten vormden een goede aanvulling op het eigenlijke onderzoek en zijn vrijwel zonder uitzondering terug te vinden in dit proefschrift. Daarnaast heeft Annet Kroon als onderdeel van haar stage meegeholpen bij het uitwerken van de visgegevens.

Bij deze wil ik ook graag een woord van dank en waardering richten aan de leden van de voormalige begeleidingsgroep van het ZOWEC-vissenprojekt, zijnde Drs. Rob Lambeck (DIHO), Prof. Dr. Niels Daan (RIVO), Dr. Bouwe Kuipers (NIOZ), Ir. Bert Steinmetz (Directie van de Visserijen), Drs. Wim van Densen (Landbouwuniversiteit Wageningen) en Drs. Cees Peeters (DGW, Rijkswaterstaat). Elke keer weer bleken zij bereid om onderzoeksvoorstellen, voorlopige resultaten, koncept-artikelen en wat dies meer zij te

willen bestuderen en van zinnig kommentaar te willen voorzien. Met een dergelijke groep specialisten achter de hand was het voor mij bijzonder prettig en geruststellend werken.

Tenslotte wil ik nog graag Prof. Dr. Niels Daan bedanken voor de wijze waarop hij deze academische promotie voor mij heeft mogelijk gemaakt en bovenal voor het vertrouwen dat hij in mij, als zijn eerste promovendus, heeft gesteld.

En verder dank aan iedereen die wel eens heeft meegeholpen tijdens een vistocht en aan alle kollega's die op enigerlei wijze hebben bijgedragen aan het welslagen van dit proefschrift.

CHAPTER 1
HOOFDSTUK 1

SYNOPSIS

Introduction

The south-western part of The Netherlands was swept by an extreme stormflood in the night of 31 January on 1 February 1953. Approximately 1800 people drowned and tens of thousands of hectares of agricultural land were flooded. To avoid repetition of such a flooding disaster, the Dutch government decided to dam up all the estuaries in the SW Netherlands by large sea walls, with the exception of the Westerschelde, being the main sea-route to the harbour of Antwerp. In 1957 this so-called Delta Plan passed the Dutch parliament (Duursma *et al.*, 1982; Bannink *et al.*, 1984).

For hydrotechnical reasons the Grevelingen estuary was first cut off from the rivers Rhine and Meuse by building a secondary dam in the east (Grevelingendam) in 1964. In 1971 the mouth of the estuary was closed by a massive wall (Brouwersdam), precluding the influence of the North Sea in the just now created Lake Grevelingen (Bannink *et al.*, 1984).

In 1978 the connection with the North Sea was partially restored by building an under-water sluice (capacity 100 to 140 $m^3.s^{-1}$) in the western Brouwersdam, while in 1983 a siphon with a capacity of approximately 100 $m^3.s^{-1}$ (Flakkeese spuisluis) became operative in the eastern Grevelingen-dam. By manipulating the two sluices an artificial flow regime for the entire Lake Grevelingen can be aroused.

In the lake the chloride concentration decreased gradually from 17 $^0/oo$ Cl^- in 1971 to less than 13 $^0/oo$ Cl^- in 1978. Since 1979 the chlorinity is stabilized at approximately 16 $^0/oo$ Cl^- by exchanging lake-water against North Sea water during winter (mainly from mid October through February). Only in 1979 the Brouwerssluice was operated the whole year round (Bannink *et al.*, 1984).

In 1957 the Delta Institute for Hydrobiological Research was founded as part of the Royal Netherlands Academy of Arts and Sciences. The Delta Institute was established in the delta area of the SW Netherlands with the aim of studying possible environmental changes resulting from the closure of the various river mouths and sea arms in this area. Since 1970 the major objectives of the institute concern studies on ecosystem functioning in relation to large environmental changes (Duursma & Nieuwenhuize, 1985).

In 1972 the research group "Carbon cycle in the Grevelingen" of the

Delta Institute started an ecosystem study aimed at the quantification of the cycling of organic matter through the food web in the newly evolving saline lake (Nienhuis, 1978a, 1978b). However, not all aspects of the required investigations could be covered by the permanent staff of the research group (Bannink *et al.*, 1984).

In March 1979 the Director-General of Rijkswaterstaat (Ministry of Transport and Public Works) authorized a complementary study of the saline water ecology of Lake Grevelingen. Financed by the former, the actual realization of the research programme as well as the ultimate scientific responsibility of the ZOWEC (ZOut Water ECologie) project was boarded out to the Delta Institute for Hydrobiological Research, which had also been the principal originator. The ZOWEC project comprised five topics, which fitted entirely in the research programme of the working group "Carbon cycle in the Grevelingen" of the Delta Institute:

1. Mineralization of organic matter in the water column (Goossens *et al.*, 1983).
2. Mineralization of organic matter in the sediment (Lindeboom & de Klerk - van der Driessche, 1983).
3. Quantification of the role of fish in the carbon cycle (Doornbos *et al.*, 1986).
4. Aspects of sediment-water exchange (Kelderman, 1983).
5. Separation and quantification of seston (van Ierland & Peperzak, 1982).

The aim of section 3 of the project was to quantify the role of the fish in the food chain of the lake on the basis of density, growth (production), prey selection and annual food consumption, as well as their role in converting energy from the lower trophic levels (*e.g.* stored in zooplankton and zoobenthos) to the higher ones (*e.g.* available to piscivorous birds). The actual investigations have been concentrated on: 1) the food composition and food uptake of the most important fish species in the lake, and 2) the predation of the fish by their main predators.

Already since 1960 the estuaries in the SW Netherlands have been monitored regularly with a 3 m beam trawl by the Delta Institute to determine possible changes in the fish fauna with respect to the ongoing Delta Plan (*cf.* Vaas, 1970, 1979). Therefore, the most conspicuous impacts of the hydraulic engineering works on the original fish fauna of the Grevelingen could be studied as well.

In this thesis the main results of the investigations, most of which have been published earlier, have been united as separate chapters.

Results, supplemented by recent developments

In Chapter 2 a review is given concerning the changes in the fish fauna of the Grevelingen from 1960 to 1980 in relation to the hydraulic engineering works realized over the same period. The number of fish species caught by a small beam trawl decreased sharply as a consequence of the embankment in 1971. Either some species had disappeared completely from the lake or the abundance had become too low to be detected in the surveys. The number of fish species increased again after opening of the Brouwerssluice to the North Sea in 1979.

When more recent information is included, a total of 59 species belonging to 31 families have been observed in Lake Grevelingen during 1979 to 1982 (Appendix 1). This is still a rather small number compared to the approximately 100 fish species recorded in the Wadden Sea (Witte & Zijlstra, 1978) and in the Oosterschelde estuary (Doornbos *et al.*, 1981), or to the 134 species known from the Dutch coastal area (Nijssen & de Groot, 1980). The cumulative number of fish species recorded in the Dutch estuaries is very similar to the number found in similar areas in Great Britain, *e.g.* 97 species for the Severn estuary (Claridge *et al.*, 1986) and 98 species for the Thames estuary (Andrews, 1984). The comparatively small number of fish species in Lake Grevelingen appears to be a direct consequence of the enclosure from the surrounding sea areas, by which many of the errant species will not be found.

The number and biomass figures of *Pomatoschistus microps* for the entire lake, as given in Chapter 2 (Table II), will have been underestimated, since this species appeared to be predominant in the littoral zone which was not surveyed in 1980 (*cf.* Chapter 5).

The commercial yearly landings of the eel *Anguilla anguilla* are still increasing, from an average of 69 tons over 1972 to 1977 to approximately 85 tons (*i.e.* 0.8 g FW.m^{-2}) during 1979 to 1982. These figures must be regarded as minimum estimates of the annual eel production, because since 1979 part of the population can escape through the Brouwerssluice to the

North Sea in autumn, while the increasing number of cormorants *Phalacrocorax carbo* will also take their share.

According to H.W. de Nie (1987, personal communication) eels have a mean daily food intake during the growing season corresponding to about 2% (range 0.8 to 3%) of their body weight. Using a minimum annual production of 85 tons FW, a P/B ratio of 0.5 (Doornbos, 1982, 1985) and a growing season of 183 days (roughly from mid April to mid October), an annual consumption by the eel population in Lake Grevelingen would be implied of at least 622 tons FW ($\sim$ 1.0 g $ADW.m^{-2}$). This figure is of the same order of magnitude as was assessed for the flounder population in 1980 (*cf.* Doornbos & Twisk, 1984).

If the increased yield is an indication of an increase in eel biomass, the decline of the plaice and flounder stocks (*cf.* Chapter 3) should have favoured the feeding conditions for the eels, since the supply of macrozoobenthic prey has been high ($\sim$ 30 g $ADW.m^{-2}$) and fairly stable over that period (Lambeck, 1985). Possible changes in fishing effort of the professional eel fishery are unknown, but will probably not be very large. In eel stomachs remains of worms, crustaceans (especially brown shrimps *Crangon crangon* and shore crabs *Carcinus maenas*), molluscs (predominantly bivalve spat), gobiid fish and sprats *Sprattus sprattus* (only eaten by the larger eels) have been found. Unfortunately, time did not permit to study prey selection, growth and food consumption of the eels in greater detail.

In general, eels caught with the standard beam trawl (6 x 6 mm mesh size) were significantly smaller (Fig. 1) than those caught with a 50 m long pelagic trawl (having an average mouth opening of 35 m^2 in operation and 8.5 x 8.5 mm meshes in the cod-end). Moreover, it is remarkable that in 1981 and 1982 eels smaller than approximately 40 cm and 30 cm, respectively, were mainly caught with the beam trawl, while the larger specimens were caught by the pelagic trawl. This could indicate that, in addition to size differences due to mesh selection in both gears, during summer at least part of the larger eels lived predominantly pelagically.

Atherina boyeri was not observed any longer since 1979. Probably the big-scale sand-smelt prefers low salinities (*cf.* Wheeler, 1978), since the species was still present in the nearby brackish Lake Veere (P. de Koeijer, personal communication). However, on the basis of multivariate analyses conducted on a series of morphometric and meristic characteristics of sand-smelts from populations around the British Isles Bamber & Henderson (1985)

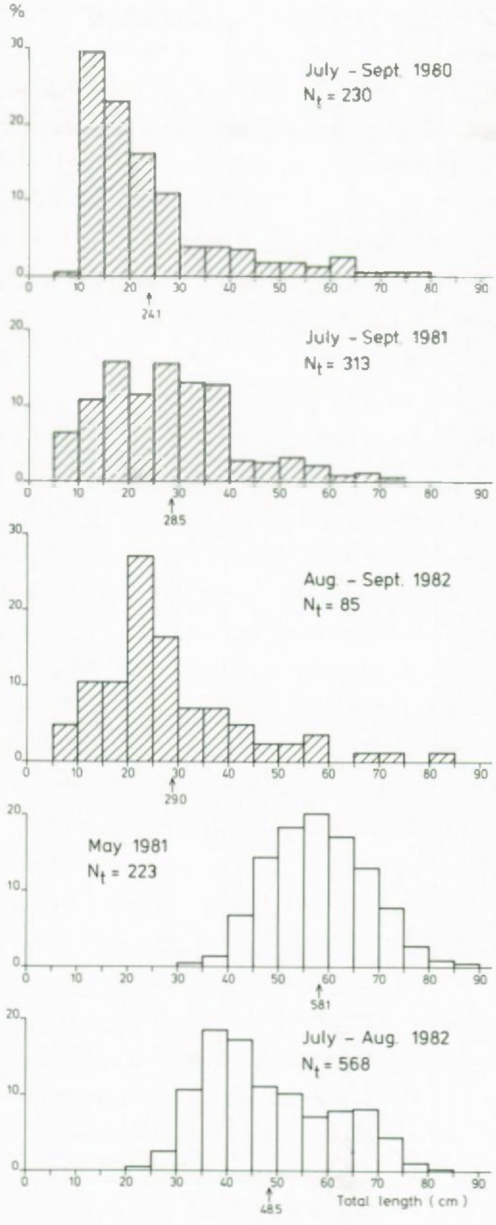


Fig. 1. Size-frequency distribution of eel in Lake Grevelingen during 1980 to 1982, caught with a beam trawl (hatched) and with a pelagic trawl (white). The average length of each group is indicated by an arrow.

showed recently that the two species *Atherina presbyter* and *A. boyeri* do actually reflect the tails of a continuum of form, and therefore conclude that it is more appropriate to consider them as the single species *Atherina boyeri*. They also conclude that the *A. boyeri* morphology varies widely under the influence of temperature and salinity conditions during embryonic development. In particular by isolation, *e.g.* in enclosed bodies of water, populations can maintain comparative morphological distinctions resulting from local selection and random genetic drift. This probably applies to the Lake Grevelingen population of sand-smelts.

In Chapter 3 the status of the dominant flatfish species in the lake, plaice and flounder, is assessed on the basis of density, population structure, growth, diet and annual food consumption.

After the embankment in 1971 the landlocked fish did not propagate successfully leading to ageing populations. Based on the constant decline in the number of plaice caught per unit of effort, a yearly mortality of 33% was estimated. In spite of the decreasing numbers the biomass initially increased, due to a fast growth, to a maximum of approximately 1100 tons (10.2 g $FW.m^{-2}$) in 1974 (Doornbos, 1985).

From 1979 through 1981 both flatfish populations were dominated by the 1979 year class. Presumably these fish entered as larvae through the Brouwerssluice, which stood open to the North Sea all over 1979. However, the pronounced position of the 1979 year class started to diminish in 1982 (see also Figs 2 and 3). Even after the improved recruitment of 1979, the number of plaice present during the study was only a fraction of the reconstructed population size in the year of closure, which may be considered representative for the former estuary.

Since the relative large fish (compared with estuarine populations) grew excellent the combined plaice and flounder consumption per year was still substantial, *i.e.* 2.8 g $ADW.m^{-2}$ in 1980 and 1.9 $g.m^{-2}$ in 1981, respectively. During the two years the consumption by plaice was almost 1.6 g $ADW.m^{-2}$. In 1971 the reconstructed biomass figure for plaice amounted to approximately 8.3 g $FW.m^{-2}$ (Doornbos, 1985), being 5.5 times higher than the average biomass value over 1980 to 1981 (*i.e.* 1.5 g $FW.m^{-2}$). Using this ratio and assuming a similar food conversion during the two periods, an annual food consumption by the plaice population would be implied of roughly 9 g $ADW.m^{-2}$ for 1971. This figure should represent the estuarine situation, since the Grevelingen was enclosed in May 1971. On the intertidal flats of the Balgzand area (western Wadden Sea) Kuipers (1977) and de Vlas (1979) found an annual food intake for juvenile plaice of approximately 5 to 6 g $ADW.m^{-2}$. For the intertidal area of the former Grevelingen estuary Wolff *et al.* (1981) have estimated a food intake by II-group plaice only of 1.5 g $ADW.m^{-2}$ over the period March to May 1971, of which a total annual consumption of roughly 4 g $ADW.m^{-2}$ can be deduced. Thus, an annual consumption of 9 g $ADW.m^{-2}$ as estimated for the "estuarine situation" of 1971 does not seem unrealistically high.

Polychaete worms proved to be eaten most, *i.e.* on average 56% by weight in plaice and 45% in flounder, although some differences were noticed between the 1980 and 1981 diets.

Since 1980 the Brouwerssluice is operated mainly from about mid October to 1 March (Table 1). In principle this regime allows older plaice and flounder to migrate to the North Sea in autumn (Steinmetz & Slothouwer, 1979; Doornbos, 1981; Klein Breteler, 1986; *cf.* Figs 2a and 2b; *cf.* Figs 3a and 3b), but prevents on the other hand late arriving larvae to be flushed into the lake since the main concentrations of pelagic plaice larvae appear at the entrance of the estuaries in March and April, and those of flounder as late as April (Rijnsdorp *et al.*, 1985; van der Veer, 1985).

Table 1. Number development of plaice in Lake Grevelingen during 1979 to 1985 (and hence, after the Brouwerssluice became operative in 1978) based on the stock assessments around mid September of each year, and the estimated (for procedure see Doornbos & Twisk, 1984) number of immigrated plaice larvae during each spring. After own data (1979 to 1982) and those of Klein Breteler (1986).

Year	Brouwerssluice open	0-group (x 10^6)	≥ 1 year (x 10^6)	Total (x 10^6)	Number of immigr. larvae (x 10^6)
1979	4 Dec. '78 –	1.5	0.5	2.0	10.3
1980	– 1 March '80	0.1	1.2	1.3	0.8
1981	mid Oct. '80 - 1 April '81	0.2	0.7	0.9	1.4
1982	mid Oct. '81 - 11 March '82	0.2	0.4	0.6	1.5
1983	mid Oct. '82 - 1 March '83	0.1	0.2	0.3	0.8
1984	mid Oct. '83 - 1 March '84	0.1	0.2	0.3	0.8
1985	mid Oct. '84 - 22 March '85	0.7	0.2	0.9	4.8

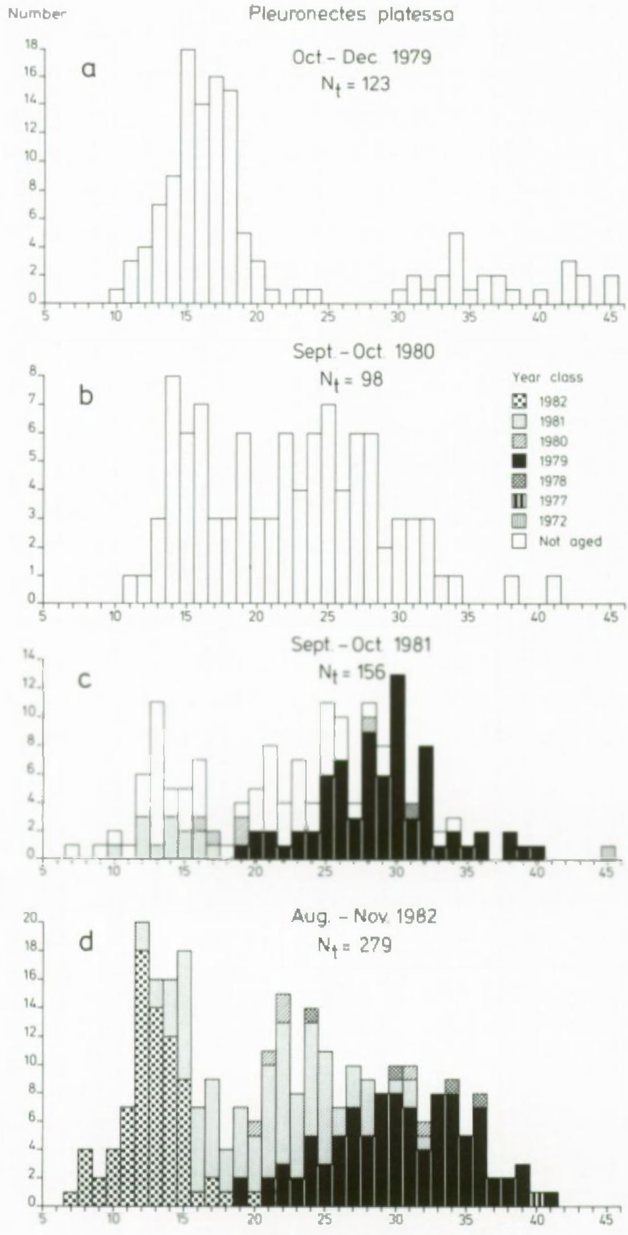


Fig. 2. Length-frequency distribution of plaice in: a) 1979, b) 1980, c) 1981 and d) 1982. The fish from 1981 (partly) and 1982 were also aged.

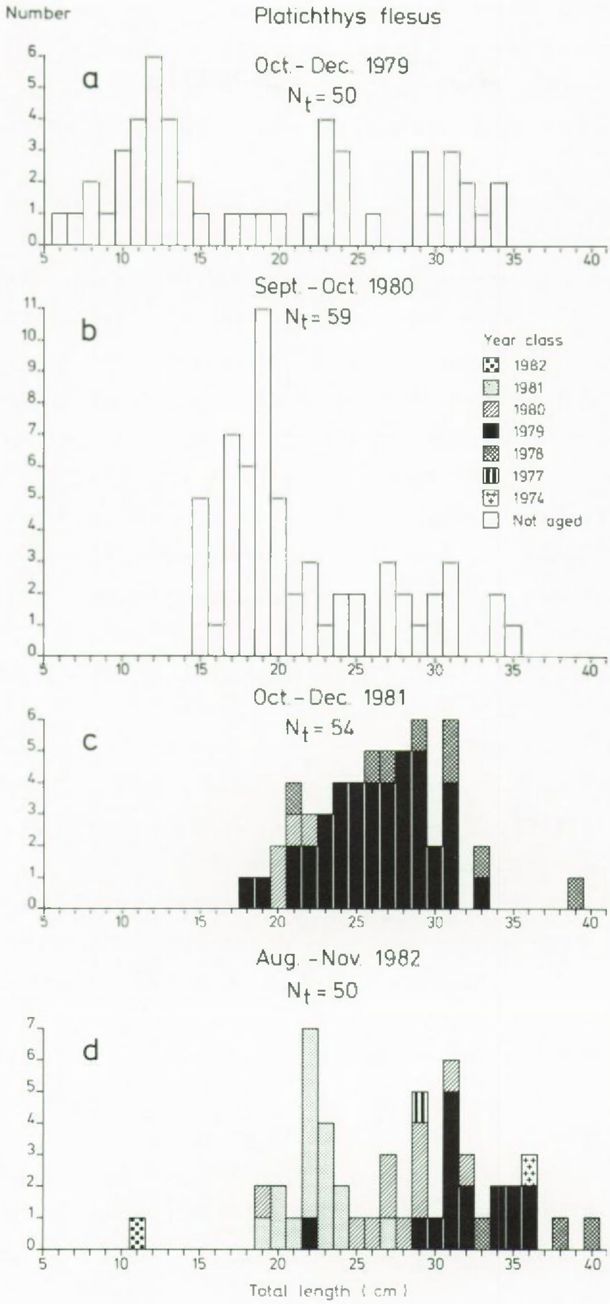


Fig. 3. Length-frequency distribution of flounder in: a) 1979, b) 1980, c) 1981 and d) 1982. The fish from 1981 and 1982 were also aged.

As could be expected, the sluice management adopted resulted in a constant decline of the plaice population ever since the slight recovery in 1979 (Klein Breteler, 1986; Table 1). However, in contrast to the previous years the Brouwerssluice was operated in the spring of 1985 until 22 March. This resulted in a relatively high number of settling larvae and the decline of the plaice stock in the lake was halted. Uptake of North Sea water through the Brouwerssluice in combination with a discharge of the surplus of lake-water through the newly built "Flakkeese spuisluis" in the eastern Grevelingendam in the spring of 1985 has apparently resulted in a relatively higher retention of plaice larvae from the coastal water (Table 1). These data underline once again that the Brouwerssluice has to be operated in spring through April, preferably in combination with the "Flakkeese spuisluis", to improve recruitment and build up the plaice density in the lake (*cf.* Doornbos, 1985).

Of course, the settlement in any one year will still depend on the strength of that particular year class in the North Sea. In plaice weak and strong year classes may differ one order of magnitude (*cf.* Zijlstra *et al.*, 1982; Anonymous, 1982, 1984, 1985) and similar differences in annual recruitment to the Grevelingen could be expected.

Still, from a continuation of the present sluice management (*i.e.* mainly open until 1 March and incidentally to 1 April) it is expected that in the near future the number of plaice in Lake Grevelingen will fluctuate around 0.5 million individuals (Table 1).

For flounder the situation is even worse, since the pelagic larvae arrive in the estuaries predominantly in April (van der Veer, 1985). Consequently, no settlement of 0-group flounder was observed in the lake during 1980 to 1982 (Fig. 3). Over this period the population size decreased from 0.7 million in 1980 to approximately 0.1 million individuals in 1982. Only if the sluice would be operated well into May the flounder stock might recover to some extent, but in the present situation the numbers can only be expected to decline even further. Plaice and flounder larvae appear to be badly needed to improve the small flatfish stocks, particularly since except for eel there are only few other large predacious fish in the lake.

In Chapter 4 special attention is paid to the spectacular growth of the 0-group plaice in Lake Grevelingen. The mean lengths and weights attained here during the first growing season exceed all values given in the literature for natural habitats. The fast growth can be illustrated by comparing the lengths attained in the lake in 1981 and 1982 with those from the nearby Oosterschelde estuary in the respective years (Table 2). Only with plaice reared in experimental ponds partly supplied with warm water discharge from the Hunterston nuclear power plant (Scotland), similar or even somewhat higher growing figures were achieved (Bardach *et al.*, 1972).

Table 2. Comparison of the average lengths ($\bar{L}$ in cm ± s.d.) of 0-group plaice at the end of their first growing season in Lake Grevelingen and in the Oosterschelde estuary, the latter after data of A. Rijnsdorp (personal communication).

Year	Grevelingen	Oosterschelde
1981	13.0 ± 2.0	9.4 ± 1.5
1982	14.5 ± 3.4	8.7 ± 2.0

Since the length increment of juvenile plaice in the lake could be described well by an empirical model developed by Fonds (1979), based on rearing experiments, it was concluded that the observed fast growth was largely the result of the relatively high water temperatures. There were no indications of any density-dependent effects or that feeding conditions provided a limiting factor.

In Lake Grevelingen growth rates in flounder (year class 1979) were also exceptionally high (Table 3).

Table 3. Mean total lengths (L in cm) of flounders at the end of their first (L_1), second (L_2), third (L_3) and fourth (L_4) growing season in various European waters.

Area	L_1	L_2	L_3	L_4	Reference
Lake Grevelingen	11.2	~18.5	26.3	31.5	This study
River Frome	8.9	15.1	22.5	30.4	Beaumont & Mann, 1984
Taymar estuary	7.6	14.7	20.5	28.9	Hartley, 1940
Ythan estuary	7.4	15.0	21.9	27.2	Summers, 1979
Baltic Sea	-	11.5	16.0	19.5	Kandler, 1932[1)]
Baltic Sea	4.4	11.1	16.3	20.1	Cieglewicz *et al.*, 1969[1)]

1) *Vide* Beaumont & Mann (1984)

In Chapter 5 the density, growth, diet and food consumption of the main Gobiidae, comprising the common goby *Pomatoschistus microps*, the sand goby *P. minutus* and to a lesser extent the black goby *Gobius niger*, are investigated. They appear to occupy a key-position in the food chain of Lake Grevelingen. In terms of quantity, the gobiids are undoubtedly the most important group of fish making energy from low trophic levels available to the higher ones.

Compared with other areas the observed densities are high while growth is fairly good. As a consequence annual consumption, accounted for largely by copepods (roughly 90% by weight) and other small epibenthic crustaceans, is substantial, *i.e.* at maximum 3.5 g $ADW.m^{-2}.a^{-1}$ for both gobiid populations combined. In turn, the gobiids suffer from a high mortality. They proved to be eaten by a variety of predators: various flatfish species (*i.e.* plaice, flounder, dab *Limanda limanda*, turbot *Scophthalmus maximus* and brill *S. rhombus*), eel, bull-rout *Myoxocephalus scorpius*, herring *Clupea harengus*, viviparous blenny *Zoarces viviparus* and piscivorous birds. For instance, during 1981/1982 the food of the migrating and wintering populations of the great crested grebe *Podiceps cristatus* and the red-breasted merganser *Mergus serrator* consisted for 60% (by weight) of gobiid fish. A combined estimate for the bird and flatfish predation indicates that these account for 60% in the reduction of the standing stocks of the gobiids present in late summer (see also Chapter 6).

It is not quite clear yet what causes the observed yearly fluctuations in the gobiid densities. The decline in the *P. microps* population in 1979 might be ascribed to the severe winter in that year, after which it took almost two years for the population to recover.

In Chapter 6 the role of the piscivorous birds in the food chain of Lake Grevelingen is described on the basis of abundance, prey selection and annual food consumption. After the enclosure in 1971 the numbers of great crested grebes *Podiceps cristatus*, red-breasted mergansers *Mergus serrator* and cormorants *Phalacrocorax carbo*, using the lake as a stop-over and refuel area during part of the year, increased significantly.

After a downfall during the 1979 to 1983 period the number of wintering great crested grebes seems to return to their former abundance. This conclusion can be drawn from the number of birds counted on Lake Grevelingen during the last years (Meininger *et al.*, 1985; Fig. 4a) as well as from the estimated number of grebe-days spent on the lake (Fig. 5a). Also the number of wintering mergansers is still increasing (Fig. 4b and Fig. 5b) and to date mid winter peak counts of 2400 to 3800 birds are not uncommon. This is two to three times higher compared with the period before 1978. The largest increase, however, is certainly observed in the cormorant. Ever since 1982 the autumn peaks lie around 2000 birds (Fig. 4c), while the number of bird-days spent on the lake increased roughly four times compared with the 1972 to 1979 period (Fig. 5c).

Considering the abundance patterns in the dominant piscivorous bird species one might expect their prey species to be available in sufficient quantities. Since 1982 nothing is known about the stock developments of the small food fish. Assuming an identical weight share of 60% in the diets of the grebes and mergansers (*cf.* Chapter 6), the two bird populations should have consumed approximately 107 tons of gobiids in 1984/1985 (which was 51.5 tons in 1981/1982). Since in 1981/1982 at least 60% of the late summer stocks of the gobiids was consumed by birds and flatfishes it would seem

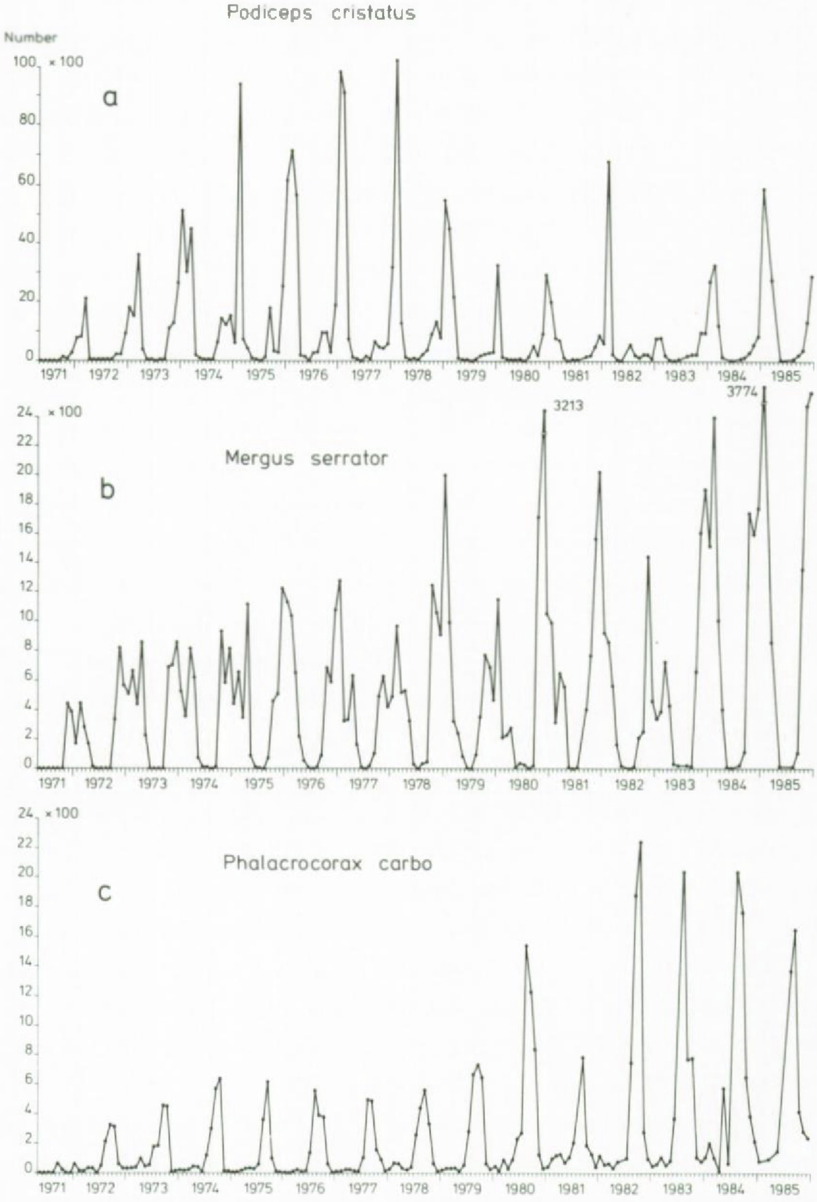


Fig. 4. Monthly peak numbers of: a) great crested grebe *Podiceps cristatus*, b) red-breasted merganser *Mergus serrator* and c) cormorant *Phalacrocorax carbo*. Data are obtained from the bird counts of Staatsbosbeheer (see also Meininger *et al.*, 1984, 1985).

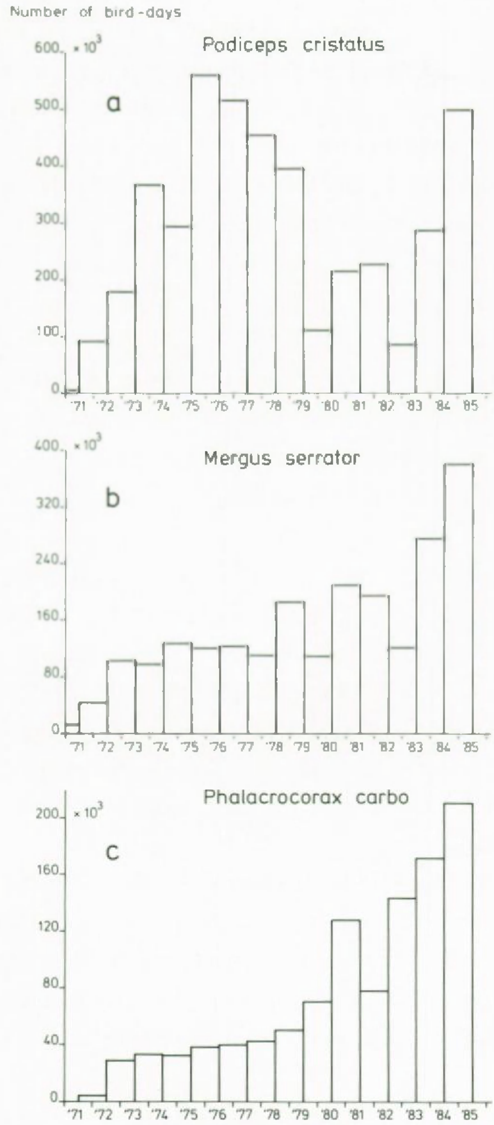


Fig. 5. Seasonal (1 July - 30 June) number of bird-days of: a) great crested grebe *Podiceps cristatus*, b) red-breasted merganser *Mergus serrator* and c) cormorant *Phalacrocorax carbo* in Lake Grevelingen during 1971 to 1985. The number of bird-days was calculated on the basis of the bird counts of Staatsbosbeheer.

that under these stock size conditions, there should have been no space for an increased predation by birds, without adverse effects on the gobiid populations. However, the marked decrease in the number of plaice and flounder (*cf.* Chapter 3) should have been associated with a reduced predation by these flatfish, leaving a greater share of the gobiid production available to the birds. Unfortunately, nothing is known about the food preference of the cormorant in Lake Grevelingen.

While in 1981/1982 the total annual fish consumption by birds was estimated at 115 tons FW (or 0.18 g ADW.m^{-2}) this has likely increased to approximately 257 tons (0.4 g ADW.m^{-2}) in 1984/1985. Hence, there is strong evidence that the impact of the piscivorous birds on the fish fauna (including epibenthic crustaceans such as shrimps) of Lake Grevelingen is still increasing. To what extent the fish fauna has responded to this increased predation can only be guessed.

Finally, in Table 4 a general view is presented of the estimated biomasses, annual production figures and yields (*c.q.* consumption figures) of the various fish species in Lake Grevelingen during the period 1980 to 1982. In these days the fish fauna is dominated (by weight) by eel *Anguilla anguilla*, while plaice *Pleuronectes platessa* has fallen back to second position. In the former Grevelingen estuary and during the first years after the embankment the biomass of the demersal fishes was dominated by plaice (Vaas, 1979).

Only 25% of the total fish biomass is estimated to belong to pelagic species. Three-spined stickleback *Gasterosteus aculeatus*, sprat *Sprattus sprattus* and sand-smelt *Atherina* sp. propagate in the lake (Doornbos, 1981, 1982), while the herring *Clupea harengus* population is supposed to originate predominantly from young fish immigrating through the Brouwers-sluice in winter.

According to published data compiled by Jansson *et al.* (1985) the biomass figures of fishes in shallow coastal waters may amount to as high as 125 g FW.m^{-2}, while annual mean values roughly range from 0.2 to 17 g FW.m^{-2}. In comparison, the overall 7.1 g FW ($\sim$ 1.2 g ADW).m^{-2} found in Lake Grevelingen is of intermediate value (Table 4).

Table 4. Overall estimates for biomass, annual production and yield (*c.q.* consumption) of the main fish species in Lake Grevelingen over 1980 to 1982 (figures are in tons fresh weight for the entire area, *i.e.* 108 km^2). When known, the main consumers of the fish are mentioned too.

Species	Biomass	Production	Yield / Consumpt.	Main consumers
Demersal				
Pleuronectes platessa	125		20	Man (Anglers)
Platichthys flesus	60		10	Man (Anglers)
Other Pleuronectiformes	35			
Anguilla anguilla	170	>85	85	Man, Birds?
Pomatoschistus microps	72	261		
Pomatoschistus minutus	85	271	102[1)] (all three gobies)	Flatfish, Birds
Gobius niger	15	∿48		
Pelagic				
Gasterosteus aculeatus	∿40		2.4[1)]	Birds
Sprattus sprattus	∿70		3.3[1)]	Birds
Clupea harengus	∿70		9.9[1)]	Birds, Anglers?
Atherina sp.	∿22		0.4[1)]	Birds
Total	764	= 7.1 g FW.m^{-2}		

1) Data for 1980/1981 only

In conclusion

Ten to 15 years after its creation the ecosystem of the saline Lake Grevelingen is still evolving. This not only applies to aspects of primary production (Nienhuis, 1985) and benthic fauna (Lambeck, 1985), but certainly also to fish.

With respect to the fish fauna a number of conclusions can be drawn from the present study:

1. The number of fish species in Lake Grevelingen is rather small.
2. There are only few fish preying on larger benthic organisms including small fish.
3. Some fish species get on very well in the saline lake, but fail to propagate successfully (*viz.* flatfish).
4. Gobiidae appear to hold a key-position in the food web of the lake. Quantitatively they are the most important group of fish making energy from lower trophic levels available to the higher ones.

To anticipate on the future developments of the fish stocks in Lake Grevelingen will necessarily be very speculative. Much will depend on the type of sluice management adopted. Ever since 1983 the manager can, apart from the Brouwerssluice in the west, also manipulate with the "Flakkeese spuisluis" in the upstream dam, allowing an artificial flow regime in the entire lake from west towards east. With proper management the fish stocks can be manipulated, although probably only on a small scale.

Up till now, a number of suggestions have been made to improve the fish stocks in the lake for commercial and recreational (angling) purposes (*cf.* Steinmetz & Slothouwer, 1979; Doornbos, 1985; Klein Breteler, 1986; Klein Breteler & Steinmetz, 1987). Since natural recruitment of eels to the lake is rather poor, it is tried to stock approximately 2500 kg elvers and/or young eels annually to compensate for the losses due to natural mortality, predation (by cormorants?) and emigration of valuable silver eels in autumn and early winter, and to improve the yields for the professional eel fishery. However, due to a scarcity on the European market this amount of elvers and young eels cannot be attained each year. Thus, a further increase in the commercial eel catches is not expected in the near future.

By taking in North Sea water through the Brouwerssluice at high tide in spring through April and discharging the surplus of lake-water through the siphon in the east at low tide, maximum numbers of plaice larvae could be flushed into the lake and allowed to settle down. To prevent emigration of older plaice during autumn or early winter the Brouwerssluice should be closed through January. When for some reason, for instance of water quality, North Sea water has to be taken in during autumn or early winter, current velocities above 1.5 $m.s^{-1}$ should be maintained because this is about the maximum swimming speed for adult plaice to maintain over a sizable distance.

Based on a number of assumptions some estimates have been made about the possible population developments of older plaice in the lake and the numbers of catchable fish for anglers (Fig. 6). As shown by these models, an equilibrium is reached after 10 to 15 years in the numbers of older plaice when the input and mortality rates are kept constant over that period. At an input of 2 million larvae per year, for instance, a stock size of older plaice ($\geqslant$ 1 year) of approximately 0.6 million fish may be expected, of which only 270,000 individuals will have an age of three years or more. In case of an annual input of 5 million larvae these figures may amount to 1.5 million and 0.7 million plaice, respectively (Fig. 6a). Because an unknown number of I-group plaice may also immigrate through the Brouwerssluice in spring, in practice a somewhat higher equilibrium could be reached in comparison with an input of exclusively larvae.

Since the legal minimum size of catchable plaice in The Netherlands is 27 cm, being reached in Lake Grevelingen in three years (*cf.* Doornbos & Twisk, 1984), the numbers of plaice to be caught by anglers can also be estimated. In case of inputs of 2 to 5 million larvae, approximately 60,000 to 160,000 adult plaice are expected to be caught annually (Fig. 6b).

Since the estimated number of immigrating larvae during 1979 to 1985 amounted only once to 10 million individuals (Table 1), such high input rates are not expected to last 10 to 15 years on end. Therefore, the corresponding stock size and catch estimates in Figure 6 do seem unrealistically high for Lake Grevelingen, even with the proposed sluice management.

During 1972 to 1977 on average 1.25 million plaice have been caught per year by anglers, with a maximum of 3.1 million fish in 1974 (Steinmetz & Slothouwer, 1979). Even allowing for an optimistic input of 5 million

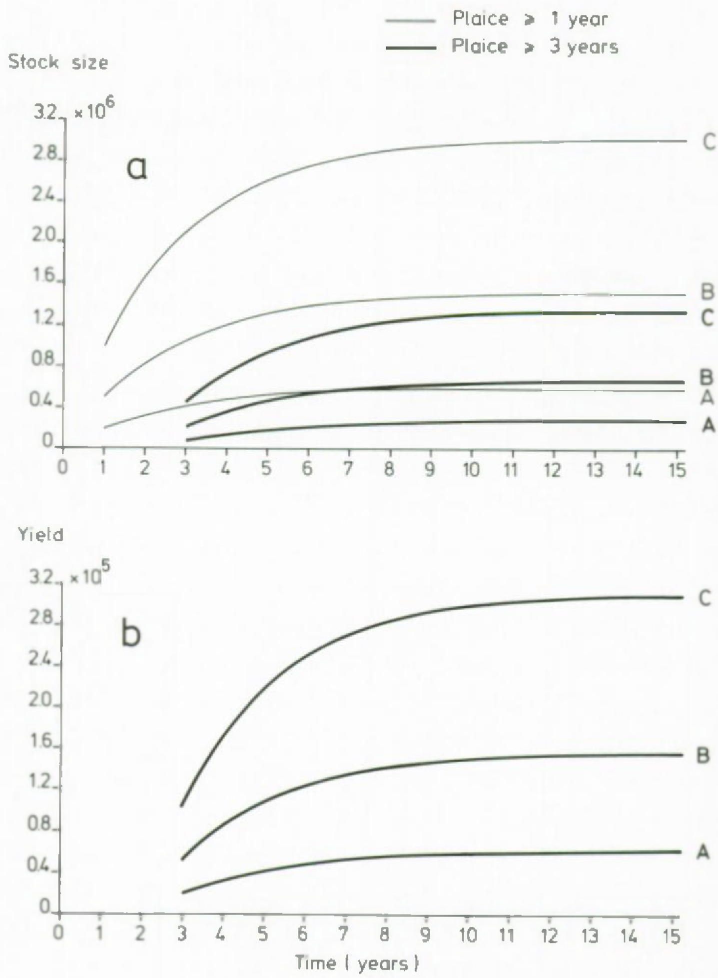


Fig. 6. Three models showing the prospected stock size developments of older plaice (a), and the expected annual yields of plaice of three years and older to be caught by anglers (b) for Lake Grevelingen. In the models A, B and C it is assumed that the input of plaice larvae during each spring amounts to 2, 5 and 10 million individuals, respectively, and that the surviving adult plaice are prevented from leaving the lake during autumn and early winter. Further, a mortality of 90% per year is assumed for juvenile plaice (< 1 year) and 33% per year for older fish. The fishery mortality is supposed to be on average 23% per year.

larvae (*cf.* Table 1) the expected annual yield of 160,000 adult plaice would be probably hardly interesting for anglers.

It has also been suggested to stock the lake with small plaice of about 5 cm and to prevent them from leaving the lake when becoming older (Doornbos, 1985). According to Klein Breteler (1986) approximately 1 million of such small fishes are required to increase the yield of adult plaice by 200,000. The current price of Hfl. 0.50 a piece implies an investment of Hfl. 2.50 for each adult plaice caught. To attain annual catches of approximately 2 million adult plaice, as were made in 1973 to 1974, would require a stocking rate of 10 million small plaice and would cost about 5 million Hfl. a year (Klein Breteler, 1986).

More recently, discussions have started to stock the lake with salmonids (Klein Breteler & Steinmetz, 1987). Young rainbow trout *Salmo gairdneri* (20 to 25 cm), smolts of sea trout *S. trutta trutta* (15 to 20 cm) or salmon *S. salar* (10 to 16 cm), or a mixture of them, could be stocked best in spring after the Brouwerssluice has been closed. In this way emigration of the fishes to the North Sea is prevented. Since the migration impulse in new smolts takes about two months, only small numbers of the fishes would probably emigrate to sea in autumn when, under the present management scheme, the sluice is opened again.

Based on an annual food supply of 1400 to 1800 tons FW available for the salmonids in the lake and presuming an overall food conversion of 5, an annual production of 300 to 350 tons of salmonids might be feasible (Klein Breteler & Steinmetz, 1987). They also calculated that, with a maximum stocking rate of 20 to 60 smolts per $ha.a^{-1}$ (depending on the species), anglers might realize maximum catches of 100,000 to 200,000 trouts or 70,000 to 150,000 salmons per year. When stocked with rainbow trout about 75% of the catch is expected to consist of adult fishes of 40 to 45 cm (0.5 to 1 kg), while in case of salmon approximately 75% should be in the range of 45 to 55 cm (1 to 2 kg) and 25% might attain a size of 65 to 75 cm (3 to 4 kg) or even somewhat more. The annual costs are expected to be in the order of 1 to 1.5 million Hfl. in case of trout and 2.5 to 3.5 million for salmon, respectively. However, the annual refunds (for instance from angler permits and the selling of fish by professional fishermen) may increase to approximately 1.5 to 2 million Hfl. for trout and as much as 4 to 5 million for salmon. Thus, they conclude that stocking with salmon would be most profitable. On the other hand, in severe winters low water temperatures could affect the survival of salmonids (especially salmon) in the saline lake seriously. Also in some summers water temperatures may become critically high (Klein Breteler & Steinmetz, 1987).

For the time being, the discussions on the improvement of the fish stocks in Lake Grevelingen will continue, especially within the working group "Salmonids in Lake Grevelingen" in which various specialists are represented (Klein Breteler & Steinmetz, 1987). But, further investigations and experiments will be needed before the first big catches may ever be landed.

References

Andrews, M.J., 1984. Thames estuary: pollution and recovery. In: P.J. Sheehan, D.R. Miller, G.C. Butler & P. Bourdeau. Effects of pollutants at the ecosystem level. John Wiley and Sons, New York: 195-227.

Anonymous, 1982. Project 1-7090 - Bestandsbepalingen jonge platvis en garnaal. Visserij *35*: 162-164.

Anonymous, 1984. Project 1-7090 - Bestandsbepalingen jonge platvis en garnaal. Visserij *37*: 232-233.

Anonymous, 1985. Report of the 0-group North Sea flatfish working group, IJmuiden, 21-25 November 1983. ICES Demersal Fish Committee C.M. 1985/G:2: 1-96.

Bamber, R.N. & P.A. Henderson, 1985. Morphological variation in British atherinids, and the status of *Atherina presbyter* Cuvier (Pisces: Atherinidae). Biol. J. Linn. Soc. *25*: 61-76.

Bannink, B.A., J.H.M. van der Meulen & P.H. Nienhuis, 1984. Lake Grevelingen: from an estuary to a saline lake. An introduction. Neth. J. Sea Res. *18*: 179-190.

Bardach, J.E., J.H. Ryther & W.O. McLarney, 1972. Aquaculture. The farming and husbandry of freshwater and marine organisms. Wiley-Interscience, New York: 1-868.

Beaumont, W.R.C. & R.H.K. Mann, 1984. The age, growth and diet of a freshwater population of the flounder, *Platichthys flesus* (L.), in southern England. J. Fish Biol. *25*: 607-616.

Claridge, P.N., I.C. Potter & M.W. Hardisty, 1986. Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn estuary. J. mar. biol. Ass. U.K. *66*: 229-258.

Doornbos, G., 1981. Verwachtingen voor de ontwikkeling van de visstand in een zoute of zoete Grevelingen tegen de achtergrond van de veranderingen die zijn opgetreden in de visfauna in de periode 1960-1980. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 81 III 6: 1-28.

Doornbos, G., 1982. Changes in the fish fauna of the former Grevelingen estuary, before and after the closure in 1971. Hydrobiol. Bull. *16*: 279-283.

Doornbos, G., 1985. Vissen in de Grevelingen. In: P.H. Nienhuis. Het Grevelingenmeer. Van estuarium naar zoutwatermeer. Delta Instituut voor Hydrobiologisch Onderzoek/Natuur en Techniek, Yerseke/ Maastricht-Brussel: 130-145.

Doornbos, G. & F. Twisk, 1984. Density, growth and annual food consumption of plaice (*Pleuronectes platessa* L.) and flounder (*Platichthys flesus* (L.)) in Lake Grevelingen, The Netherlands. Neth. J. Sea Res. *18*: 434-456.

Doornbos, G., F. Twisk, K.F. Vaas & P. de Koeijer, 1981. De visfauna van de open Oosterschelde: een inventarisatie over de periode 1960-1976. Rapporten en Verslagen Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, nr. 1981-5: 1-55.

Doornbos, G., F. Twisk & R.H. Bogaards, 1986. Kwantificering van vissen. ZOWEC III, Final Report. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 86 III 5: 1-190.

Duursma, E.K., H. Engel & T.J.M. Martens (eds.), 1982. De Nederlandse Delta. Een compromis tussen milieu en techniek in de strijd tegen het water. Natuur en Techniek, Maastricht: 1-511.

Duursma, E.K. & E.S. Nieuwenhuize (chief eds.), 1985. Delta Institute for Hydrobiological Research, Progress Report 1984. Delta Institute for Hydrobiological Research, Yerseke: 1-83.

Fonds, M., 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In: E. Naylor & R.G. Hartnoll. Cyclic phenomena in marine plants and animals. Proc. 13th Eur. Mar. Biol. Symp., Isle of Man, Great Britain. Pergamon Press, Oxford: 151-156.

Goossens, J.G.C.M., R.S. Minnaar & J.C. Verplanke, 1983. Koolstofmineralisatie in het water van het Grevelingenmeer. ZOWEC I, Final Report. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 I 5: 1-35.

Hartley, P.H.T., 1940. The Saltash tuck-net fishery and the ecology of some estuarine fishes. J. mar. biol. Ass. U.K. *24*: 1-68.

Ierland, E.T. van & L. Peperzak, 1982. Scheiding van seston. ZOWEC V, Final Report. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 82 V 5: 1-127.

Jansson, B.-O., G. Aneer & S. Nellbring, 1985. Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census. Mar. Ecol. Prog. Ser. *23*: 31-43.

Kelderman, P., 1983. Bodem-water uitwisseling in de Grevelingen. ZOWEC IV, Final Report. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 IV 5: 1-110.

Klein Breteler, P.H.M., 1986. Prognoses voor de ontwikkeling van de scholstand in een zoute Grevelingen. Visserij *39*: 16-31.

Klein Breteler, P.H.M. & B. Steinmetz, 1987. Toekomstig visstandbeheer in een zout Grevelingenmeer. Nota Werkgroep Salmoniden Grevelingenmeer: 1-52.

Kuipers, B.R., 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. Neth. J. Sea Res. *11*: 56-91.

Lambeck, R.H.D., 1985. Leven zonder getij. Bodemdieren in het Grevelingenmeer. Natuur en Techniek *53*: 916-931.

Lindeboom, H.J. & H.A.J. de Klerk - van der Driessche, 1983. C-mineralisatie op en in de bodem van de Grevelingen. ZOWEC II, Final Report. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 II 5: 1-132.

Meininger, P.L., H.J.M. Baptist & G.J. Slob, 1984. Vogeltellingen in het Deltagebied in 1975/76 - 1979/80. Rijkswaterstaat Deltadienst/Staatsbosbeheer Zeeland, Middelburg/Goes, Nota DDMI-84.23: 1-390.

Meininger, P.L., H.J.M. Baptist & G.J. Slob, 1985. Vogeltellingen in het zuidelijk Deltagebied in 1980/81 - 1983/84. Rijkswaterstaat DGW/Staatsbosbeheer Zeeland, Middelburg/Goes, Nota DGWM 85.001: 1-159.

Nie, H.W. de, 1987. Food, feeding periodicity and consumption of the eel, *Anguilla anguilla* (L.), in the shallow eutrophic Tjeukemeer (The Netherlands). Arch. Hydrobiol. (in press).

Nienhuis, P.H., 1978a. An ecosystem study in Lake Grevelingen, a former estuary in the SW Netherlands. Kieler Meeresforsch. (Sonderheft) *4*: 247-255.

Nienhuis, P.H., 1978b. Lake Grevelingen: a case study of ecosystem changes in a closed estuary. Hydrobiol. Bull. *12*: 246-259.

Nienhuis, P.H. (ed.), 1985. Het Grevelingenmeer. Van estuarium naar zoutwatermeer. Delta Instituut voor Hydrobiologisch Onderzoek/ Natuur en Techniek, Yerseke/Maastricht-Brussel: 1-177.

Nijssen, H. & S.J. de Groot, 1980. Zeevissen van de Nederlandse kust. Wet. Med. Kon. Ned. Natuurhist. Ver., Hoogwoud *143*: 1-109.

Philippart, R.J.L. & A.J.M. Meijer, 1982. Monitoring-onderzoek aan de visstand van de Grevelingen: resultaten 1980-1981. Bureau Waardenburg B.V., Culemborg: 1-64 (+ Appendixes).

Rijnsdorp, A.D., M. van Stralen & H.W. van der Veer, 1985. Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. Trans. Am. Fish. Soc. *114*: 461-470.

Steinmetz, B. & D. Slothouwer, 1979. De betekenis van de Grevelingen voor de sportvisserij. Visserijkundige waarnemingen in de jaren 1971-1977. Directie van de Visserijen, Den Haag, Documentatierapport no. 21: 1-101.

Summers, R.W., 1979. Life cycle and population ecology of the flounder *Platichthys flesus* (L.) in the Ythan estuary, Scotland. J. nat. hist. *13*: 703-723.

Vaas, K.F., 1970. Studies on the fish fauna of the newly created lake near Veere, with special emphasis on the plaice (*Pleuronectes platessa*). Neth. J. Sea Res. *5*: 50-95.

Vaas, K.F., 1979. Studies on the fish fauna of an estuary in the S.W. Netherlands, before and after its change into the stagnant, saline, Lake Grevelingen. Hydrobiol. Bull. *13*: 177-188.

Veer, H.W. van der, 1985. Impact of coelenterate predation on larval plaice *Pleuronectes platessa* and flounder *Platichthys flesus* stock in the western Wadden Sea. Mar. Ecol. Prog. Ser. *25*: 229-238.

Vlas, J. de, 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. Neth. J. Sea Res. *13*: 117-153.

Waardenburg, H.W., A.J.M. Meijer, R.J.L. Philippart & A.C. van Beek, 1984.

The hard bottom biocoenoses and the fish fauna of Lake Grevelingen, and their reactions to changes in the aquatic environment. Wat. Sci. Tech. *16*: 677-686.

Wheeler, A., 1978. Key to the fishes of northern Europe. Frederick Warne Ltd, London: 1-380.

Witte, J.Y. & J.J. Zijlstra, 1978. The species of fish occurring in the Wadden Sea. In: N. Dankers, W.J. Wolff & J.J. Zijlstra. Fishes and fisheries of the Wadden Sea. Final report of the section "Fishes and fisheries" of the Wadden Sea Working Group. Stichting Veth tot Steun aan Waddenonderzoek, Leiden: 10-19.

Wolff, W.J., M.A. Mandos & A.J.J. Sandee, 1981. Tidal migration of plaice and flounders as a feeding strategy. In: N.V. Jones & W.J. Wolff. Feeding and survival strategies of estuarine organisms. Plenum Press, New York: 159-171.

Zijlstra, J.J., R. Dapper & J.IJ. Witte, 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea Res. *15*: 250-272.

CHAPTER
HOOFDSTUK 2

HYDROBIOLOGICAL BULLETIN 16(2 - 3): 279 - 283 (1982)

CHANGES IN THE FISH FAUNA OF THE FORMER GREVELINGEN ESTUARY, BEFORE AND AFTER THE CLOSURE IN 1971 [1]

G. DOORNBOS

(Delta Institute for Hydrobiological Research, Yerseke, The Netherlands)

(SHORTENED PAPER)

Within the scope of the Delta Plan, a number of estuaries in the S.W. Netherlands has been closed off. One of those sea-arms is the Grevelingen where the following phases in the hydrotechnical works can be identified (NIENHUIS, 1978).

(1) Before 1964, the Grevelingen was an estuary, influenced in the east by the rivers Rhine and Meuse, and in the west by the North Sea, so that the chloride concentration fluctuated from 10 to 17 $^{0}/_{00}$ Cl^{-}.

(2) In 1964 the Grevelingendam was constructed on the east side, resulting in a high and fairly stable chloride concentration.

(3) In May 1971 the 6 km long Brouwersdam on the west side was completed and a new saline Lake Grevelingen of 108 km^2 was established. The chloride concentration in the lake declined from greater than 17 to less than 13 $^{0}/_{00}$ Cl^{-} in 1978.

(4) In December 1978 a sluice, built in the Brouwersdam, was brought into operation. As a consequence of the sluice management, the chloride concentration remained above 16 $^{0}/_{00}$ Cl^{-}.

The changes in the fish fauna in the successive phases were primarily studied with a 3 m beam trawl, and until 1977, only in parts deeper than 5 m (VAAS, 1979). After the closure in 1971 the number of fish species caught with this trawl declined from 31 to 18 (Fig. 1). From 1976 to 1978 this number stabilized at 20. A new species was the black goby *Gobius niger*, which underwent the same development as in the earlier created Lake Veere (VAAS *et al.*, 1975). When the connection with the North Sea had been renewed for over a whole year, the number of species increased to 26. Because the 'new' species were principally 'summerguests', *e.g.* garfish *Belone belone*, horse mackerel *Trachurus trachurus*, and thick-lipped grey mullet *Chelon labrosus*, they disappeared again one year later when the sluice was closed from March through the middle of October.

Before 1971, the Shannon-Weaver index was high, then in 1972 decreased as a consequence of the damming (Fig. 1). After a while, the index stabilized. However, even before the opening of the sluice, the index was declining, probably induced by the low chloride concentration at that time, and later on enhanced by the manipulation of the sluice. As mentioned above, some species were migrating into the lake, but they were scarce in number. The whole system seemed once again to be destabilized.

It should be mentioned that a beam trawl developed for demersal fish is not suitable for providing a complete picture of the fish fauna in an area. For the period 1900-1980, a total of 57 species have been recorded for the Grevelingen, of which 44 were trapped by the beam trawl (DOORNBOS, 1981).

After the closure, the number of small pelagic fish, *e.g.* sand-smelt *Atherina presbyter*, three-spined stickleback *Gasterosteus aculeatus* and sprat *Sprattus sprattus* increased enormously (Fig. 2). Only the stickleback density remained high. This species can still find a very suitable breeding habitat in the extensive *Chaetomorpha* and *Zostera* meadows. It is likely that in 1971 a large population of sprat was enclosed and reproduced in the lake during the first years. But as the chloride concentration decreased, reproduction must have ceased. In 1980 and 1981, when

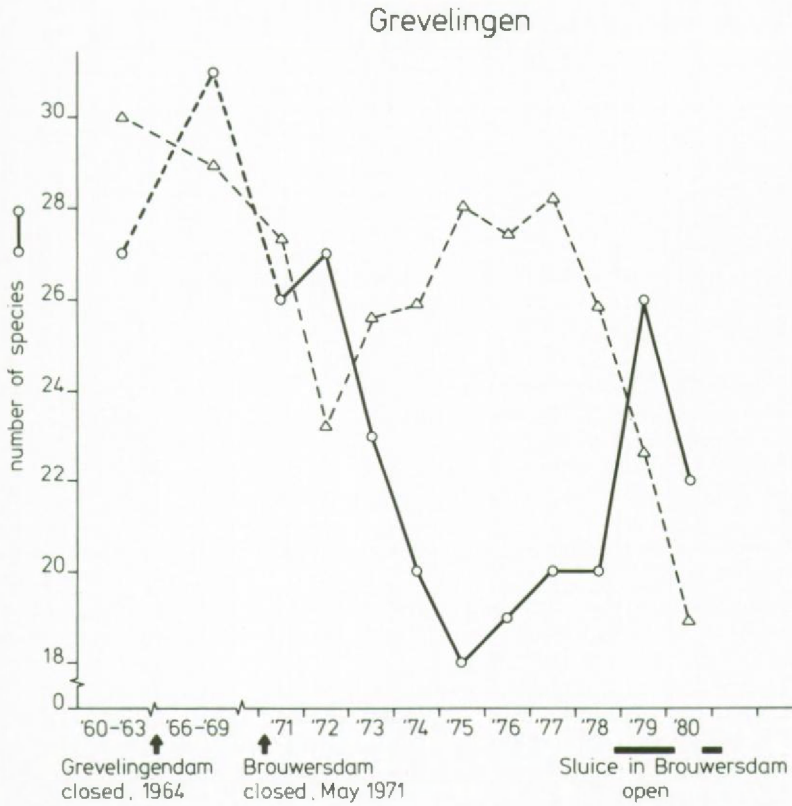


Fig. 1. Number of fish species caught with a 3 m beam trawl in the deeper parts (>5 m) of the Grevelingen and the Shannon-Weaver diversity index.

the chloride concentration was again above 16 $^{0}/_{00}$ Cl^{-}, indeed ripe female sprats and larvae were observed. The black goby, common goby *Pomatoschistus microps* and sand goby *P.minutus* have also increased, especially during 1978 to 1980, although the common goby appears to have suffered from the severe winter of 1978/1979. Regarding the flatfish, it is obvious that the sole *Solea solea*, one of the most abundant species in the estuary, disappeared very soon after the closure, probably as a consequence of the lower winter temperatures in the lake (FONDS, 1976). Both plaice *Pleuronectes platessa* and flounder *Platichthys flesus* did not recruit in the lake although the animals bear ripe spawn and milt during autumn and early winter (VAAS, 1979). About 75 % of the encaptured plaice belonged to yearclass 1971 (STEINMETZ and SLOTHOUWER, 1979). When in 1979 the sluice was opened for a whole year the plaice population was rejuvenated, the few remaining old animals left the lake in winter to migrate to their spawning places in the North Sea, and the larvae came in the spring. In 1980 and 1981 hardly any juvenile plaice of that particular year was caught, probably due to the early closing dates of the sluice, at the end of February and at the end of March respectively. In September/October 1981, 79 % still belonged to yearclass 1979 and only 14 % to yearclass 1981, which is the reverse estuarine picture.

With an appropriate sluice management one can find plaice and flounder in the lake, although the numbers will still be much lower than those in the estuary. From surveys covering the entire lake, we assessed the plaice population in the autumn of 1980 and 1981 at 1.1 and 0.9

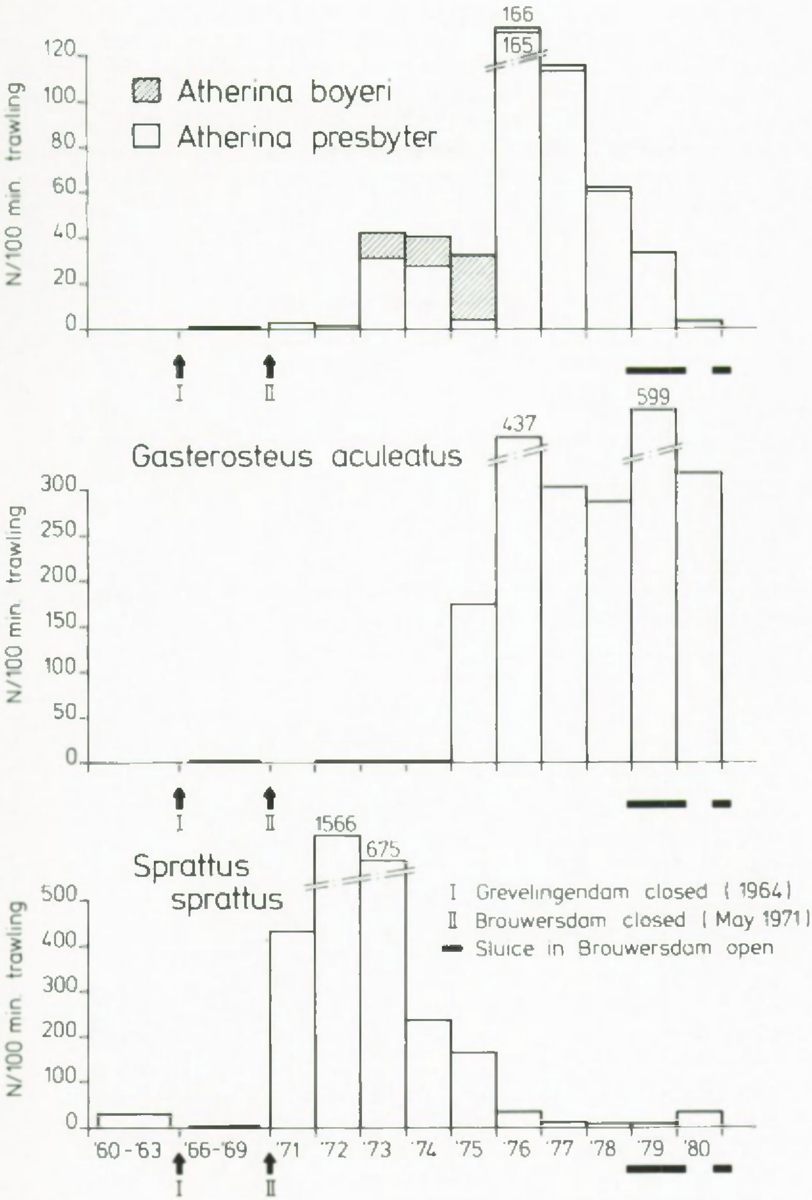


Fig. 2. Number (N) of sand-smelt *Atherina* spp., three-spined stickleback *G.aculeatus* and sprat *S.sprattus* caught per 100 minute trawling interval in the deeper parts of the Grevelingen.

million individuals, respectively. Comparison of the September data of the Directorate of Fisheries and the mean data for August-November of the Delta Institute, both expressed as numbers of individuals caught per 100 minute trawling intervals on a logarithmic scale, leads to a highly significant negative correlation between the numbers caught and the time (years). The extrapolated population size for September 1971 amounts to 14 million, assuming that from the autumn of 1972 onwards all individuals stayed at a depth greater than 5 m (= 38 km^2) and that the trawls have a fishing efficiency of 10 %. As a consequence of these 14 million animals present in the lake in September 1971, of which 10.5 million (75 %) should have been O^+ fish, and assuming a juvenile mortality of 50 % there must have been an import of at least 20 million larvae as of the 3rd of May. In the period 1972 to 1977 an estimated 7.5 million plaice were caught by sport fishermen (STEINMETZ and SLOTHOUWER, 1979). At the end of 1978 not more than 0.9 million were alive.

	Biomass percentages in total trawl catches		
species	1960 - 1969	1975 - 1976	1980
Pleuronectiformes	70.1	84.3	40.1
Pleuronectes platessa	40.2	69.9	22.1
Gobiidae	4.2	4.9	40.9
Pomatoschistus minutus	4.1	3.2	32.8
Gobius niger	–	1.0	8.0

Table I. Changes in biomass ratios in the beam trawl catches in the deeper parts of the Grevelingen, before and after the closure in 1971.

species	number ($x10^6$)	biomass (tons)
pelagic		
Gasterosteus aculeatus	120	100
Sprattus sprattus	3.4	10
Clupea harengus	0.1	1
Atherina presbyter	1.5	2
demersal		
Pleuronectes platessa	1.1	184
Platichthys flesus	0.5	69
Pomatoschistus microps	7	4
Pomatoschistus minutus	145	102
Gobius niger	4	22
Anguilla anguilla		138 *
		632 = 5.9 g $FW.m^{-2}$

Table II. Estimation of number and biomass (B) of most important fish species in Lake Grevelingen, October 1980. FW = fresh weight.

* Based on commercial yearly landings in the period 1972-1977 (=P) and $P/\bar{B} = 0.5$.

Another interesting aspect of Grevelingen plaice is its fast growth. At the end of their first summer, the average length of a young plaice is 13.0 cm (range 7 - 17 cm), which is about 3 cm longer than in the Dutch Wadden Sea (KUIPERS, 1977; DE VLAS, 1979). There are three explanations for this phenomenon. (1) In summer, the water temperature of Lake Grevelingen is somewhat higher than in the Wadden Sea and may rise well above 20°C. (2) The density of plaice and other flatfish, and hence competition for food, is low. (3) The absence of tide implies that the animals can fourage the whole day. In addition, they don't need to make energy-consuming tidal migration movements as in an estuary (KUIPERS, 1977).

Not only the number of species and the number of individuals have changed in the course of time but the biomass ratios of the demersal species have also changed (Table I). The role of flatfish, of which plaice was a dominant species, has been taken over by gobiid fishes.

Finally, an attempt has been made to quantify the number and biomass of the most important species in the lake (Table II). It is obvious that the composition of the fish fauna has drastically changed from larger to smaller species, the diversity has decreased and food chains have become shorter (VAAS, 1979).

[1] Communication no. 242 of the Delta Institute for Hydrobiological Research.

REFERENCES

DE VLAS, J., 1979. Annual food intake by plaice and flounder in a tidal area in the Dutch Wadden Sea, with special reference to consumption on regenerating parts of macrobenthic prey. Neth.J.Sea Res., 13:117-153.

DOORNBOS, G., 1981. Verwachtingen voor de ontwikkeling van de visstand in een zoute of zoete Grevelingen tegen de achtergrond van de veranderingen die zijn opgetreden in de visfauna in de periode 1960 -1980. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke and Deltadienst, Middelburg. (Unpubl. report).

FONDS, M., 1976. The influence of temperature and salinity on growth of young sole, *Solea solea* L. In: Persoone, G. and E. Jaspers, Eds., Proc. 10th Eur.Mar.Biol.Symp., Ostend, Belgium, Vol. 1:109 -125. Universa Press, Wetteren.

KUIPERS, B.R., 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. Neth. J.Sea Res., 11:56 -91.

NIENHUIS, P.H., 1978. Lake Grevelingen: a case study of ecosystem changes in a closed estuary. Hydrobiol.Bull., 12:246-259.

STEINMETZ, B., and D.SLOTHOUWER, 1979. De betekenis van de Grevelingen voor de sportvisserij. Visserijkundige waarnemingen in de jaren 1971-1977. Directie van de Visserijen, Den Haag. (Unpubl. report).

VAAS, K.F., 1979. Studies on the fish fauna of an estuary in the S.W. Netherlands, before and after its change into the stagnant, saline Lake Grevelingen. Hydrobiol.Bull. 13:177-188.

VAAS, K.F., A.G.VLASBLOM and P. DE KOEIJER, 1975. Studies on the black goby (*Gobius niger*, Gobiidae, Pisces) in the Veerse Meer, SW Netherlands. Neth.J.Sea Res., 9:56 -68.

CHAPTER 3
HOOFDSTUK

Netherlands Journal of Sea Research
18 (3/4): 434-456 (1984)

DENSITY, GROWTH AND ANNUAL FOOD CONSUMPTION OF PLAICE (PLEURONECTES PLATESSA L.) AND FLOUNDER (PLATICHTHYS FLESUS (L.)) IN LAKE GREVELINGEN, THE NETHERLANDS*

by

G. DOORNBOS and F. TWISK

Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA Yerseke, The Netherlands

CONTENTS

1. INTRODUCTION

In the former Grevelingen estuary the fish fauna was dominated by flatfish, particularly plaice *Pleuronectes platessa* and sole *Solea solea* (VAAS, 1979; DOORNBOS, 1982). After the construction of the eastern Grevelingendam (1964), which cut off the open connection with the rivers Rhine and Meuse, the stock of sole decreased while those of plaice and dab *Limanda limanda* increased. Two years after the creation of the saline Lake Grevelingen (1971) sole had completely disappeared, probably due to the lower temperatures during winter, values falling below −1°C not being unusual (*cf.* FONDS, 1976).

In the saline lake, the landlocked plaice and flounder *Platichthys flesus* did not propagate successfully leading to aging populations (VAAS, 1979). Although at first numbers decreased, total biomass initially in-

* Communication no. 279 of the Delta Institute for Hydrobiological Research, Yerseke, The Netherlands

creased (DOORNBOS, 1982). After 1976, however, the share of plaice in the demersal fish community started to decline due to heavy sport fishing. A release of 160 000 plaice, 350 000 flounders and 1 000 000 dabs could not compensate the 7.5 million plaice and 1.5 million flounders angled between 1972-1977 (STEINMETZ & SLOTHOUWER, 1979, 1980).

From December 1978 through February 1980 and from 13 October 1980 through March 1981 (excluding a short period in October and November 1980), the Grevelingen was again connected to the North Sea by a new sluice in the Brouwersdam (capacity 100 $m^3 \cdot s^{-1}$) allowing limited fish migrations in and out the lake.

Since 1971, the carbon budget of the Lake Grevelingen ecosystem has been investigated (NIENHUIS, 1978a, 1978b). The aim of the present study is to assess the role of plaice and flounder in the food chains of the lake on the basis of density, growth and annual food consumption of both flatfish species during October 1979 to December 1981. The investigation forms part of a 4-year study on the quantitative importance of the fish fauna in the energy budget of Lake Grevelingen.

Acknowledgements.—This study was part of the ZOWEC project (saline water ecology) and financed by the Deltadienst of Rijkswaterstaat. We are much indebted to those assisting in the field and in the laboratory, and to those who gave valuable advice and support. We especially want to mention: W.J.L. Robër and P. de Koeijer of the research vessel "Maris Stella", Dr A.G. Vlasblom and J.J. Guerand for biomathematics, Mrs M.J. van Leerdam-de Dreu for the typing, A.A. Bolsius for making the final drawings and Mrs P. Pollen-Lindeboom for correcting the English text.

Preliminary research was done by H. Vernij, while R.H. Bogaards assisted with the fishing surveys and did most of the laboratory analyses (determination of prey items, age reading of otoliths, preparing data for computer, etc.). Dr N. Daan, Dr B.R. Kuipers, R.H.D. Lambeck, A. Rijnsdorp and J. de Vlas gave comments on the first draft of the manuscript.

2. MATERIAL AND METHODS

The essential data have been collected during trawling surveys. In the deeper parts (>2 m) of the lake fishing was done on the 18 m motor vessel "Maris Stella" which is equipped with a 3 metre beam trawl covering at standard speed a trawling area of 250 m^2 per minute. In the littoral zone a small 1.9 metre beam trawl (KUIPERS, 1975), which covers 197 m^2 per minute, was used on the 6½ m flat-bottomed boat

"Riekus". The foot rope of both nets was made heavier by an iron chain. Fine-meshed netting (10 mm and 12 mm full-mesh size in the cod-end of the 1.9 m and 3 m trawl, respectively) was used since the surveys were also intended to obtain data on small-sized fish species, particularly Gobiidae.

When possible, surveys were made twice a month. As a consequence of the abundant stocks of eelgrass *Zostera marina*, large algae, *e.g. Chaetomorpha* sp., and mussels *Mytilus edulis*, short hauls of only 2 and 2½ minutes were made with the 3 m and 1.9 m trawl, respectively. For the same reason, only 41 to 48 stations of fixed positions, distributed over three depth strata, 0 to 2 m (43 km^2), 2 to 5 m (27 km^2) and >5 m (38 km^2), were fished (Fig. 1).

In 1981 a strong decline in the eelgrass vegetation and in the bycatch of mussels allowed us to increase the number and duration of hauls from July onwards. Moreover, the gear efficiency was improved by using one tickler chain. The more favourable field situation also allowed for change towards a stratified random sampling scheme that was based upon a 500 × 500 m^2 grid over the lake; from a statistical point of view, this is more satisfactory. The deep stratum was split up into a 5 to

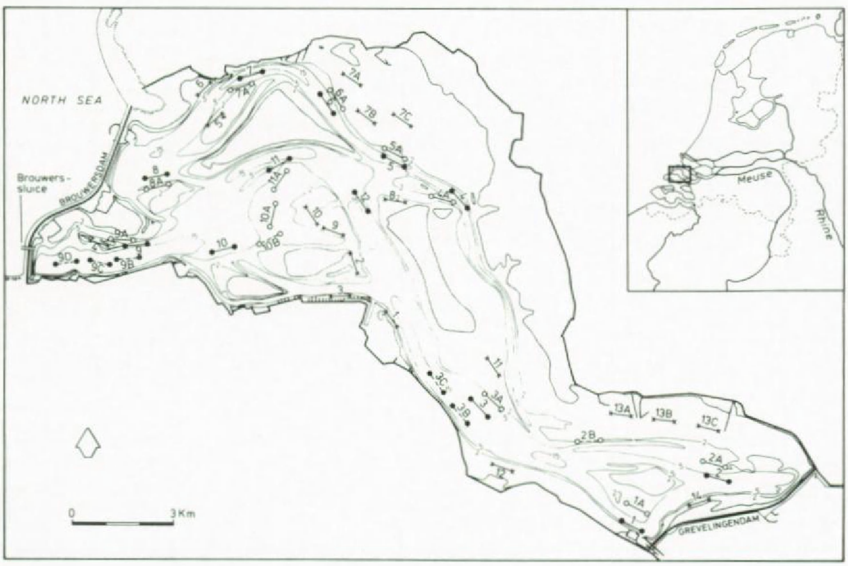


Fig. 1. Map of Lake Grevelingen (SW Netherlands), showing the positions of the fixed sampling stations in the strata 0 to 2 m (x—x), 2 to 5 m (O—O) and >5 m (●—●), and of incidentally sampled stations (indicated by interrupted lines). Depth lines in metres; areas above 0 m shaded.

15 m (27 km^2) and a deeper than 15 m (11 km^2) zone, since evidence had been obtained that the fish accumulated in the deepest part of the lake during winter time (*cf.* Chapter 3).

Sex was determined and total body length measured for all individuals caught while in the field. The larger specimens were weighed individually. The weights of those less than 50 g were obtained either by weighing them at the laboratory (in the case of some) or by reconstruction on the basis of an established length-weight relationship of a subsample. In the spring of 1980 and the autumn of 1981 otolith samples were taken for age reading.

Applying KUIPERS' (1975) method, the overall efficiency of the 3 m trawl for plaice has been estimated at about 10% with 0 and at 20% with 1 tickler chain. No significant differences were found between size classes. For the 1.9 m beam trawl with 1 tickler chain, an efficiency of 10%, as determined for the same net equipment by KUIPERS (1975) for plaice >20 cm, has been used. An efficiency of 6% has been assumed in the absence of a tickler chain. The same values have been applied for flounder.

Immediately after the catch, the stomachs of the fish were preserved in 4% formalin. In the laboratory, the prey items were identified to species level as far as possible. The ash-free dry weight (ADW) of the prey remains was determined in 1981 only. The counted number of prey items in the 1980 samples were converted into ADW values on the basis of the mean ADW per prey species in the 1981 samples.

Because energy requirements of fish are a function of size, the plaice were divided into size classes (WINBERG, 1956; DE VLAS, 1979). The small O-group plaice caught during 1981 could easily be distinguished the whole year round and have been treated separately. Per sampling date the older animals were equally divided into 3 weight classes: light, medium and heavy. Therefore, each weight class does not represent a year class, but a group of animals with presumably the same energy demands and probably feeding on about the same size of prey. Stomach contents of animals from one weight class were pooled. For each class, growth was computed by regression analysis under the assumption that fast growers remain fast growers (WINBERG, 1956). No such split was made in the case of flounders, since they were less numerous.

Annual food consumption (F_A) of the plaice and flounder population was estimated by the equation:

$$F_A = \sum_{j=1}^{m} p_j \cdot F_j$$

where m is the number of representative periods in the year, p_j is the number of days in period j, and F_j is the food intake in grams ADW per m² per day of all weight classes together in the period j. A representative period is defined by consecutive midpoints between sampling dates; and the food demands, prey composition and water temperature at the sampling date included within the period is supposed to reflect the average situation over this time span (DE VLAS, 1979).

F_j was calculated on the basis of a slightly simplified formula of DE VLAS (1979), which substitutes L^3C by W, where L is length, C is a condition factor and W is the fresh weight of the fish:

$$F_j = \sum_{i=1}^{n} 0.17\, d_i \{2\,(W_2 - W_1)_{ij}\, p_j^{-1} + 0.02\, W_{ij}^{0.8} \cdot 2^{0.1 T_j}\}$$

where n is the number of weight classes, d_i is the density per m² of weight class i, W_{ij} is the fresh weight in g of weight class i at the sampling date in period j, $(W_2 - W_1)_{ij}$ is the difference in computed fresh weights in g of weight class i between start and end of the representative period j, T_j is the water temperature in °C at the sampling date in period j, and 0.17 is the assumed ratio between ash-free dry and wet weight of the food.

The contribution of the different food species was estimated on the basis of the stomach contents and the calculated food demands of the plaice and flounder population.

The total number of fish, the density of fish per m² and the 95% confidence limits were estimated by the method of stratified (random)

TABLE 1
Age composition of plaice and flounder population during 1980 and 1981. Data for 1980 are from VERNIJ (1983).

Year class	Plaice				Flounder			
	Feb.-July 1980		*July-Dec. 1981*		*Feb.-July 1980*		*July-Dec. 1981*	
	Number	*%*	*Number*	*%*	*Number*	*%*	*Number*	*%*
1981	–	–	33	9.4	–	–	–	–
1980	–	–	30	8.6	–	–	4	7.4
1979	118	80.8	281	80.3	33	43.4	42	77.8
1978	18	12.3	5	1.4	27	35.5	8	14.8
1977	6	4.1	–	–	7	9.2	–	–
1976	2	1.4	–	–	5	6.6	–	–
1975	–	–	–	–	3	4.0	–	–
1974	1	0.7	–	–	1	1.3	–	–
1973	1	0.7	–	–	–	–	–	–
1972	–	–	1	0.3	–	–	–	–
Total	146	100	350	100	76	100	54	100

sampling (SAMPFORD, 1962; COCHRAN, 1963). The consumption and its confidence limits were calculated from the density and its confidence limits by means of the above formula.

3. RESULTS

3.1. POPULATION DYNAMICS AND GROWTH RATES

3.1.1. PLAICE

At the end of the year 1979, during which the Brouwerssluice (Fig. 1) was operative almost constantly, the length-frequency distribution of plaice was rather disjunct (Fig. 2a). Almost 80% of the population was smaller than 25 cm. The remaining 20% were large plaice of 30 to 45 cm, presumably representing survivors of the population landlocked in 1971 and the animals released in the years 1975 to 1978. Since during the first half of 1980 plaice population consisted of the year class 1979 (81%) and of 1978 (12%), whereas nearly all older plaice had vanished at that time (Table 1), the majority of the animals smaller than 20 cm must have belonged to the year class 1979.

Up to July 1980 no O-group plaice were caught. No age composition has been determined for the second half of 1980, but the share of O-group animals in 1980 has been much smaller than in the previous year (Fig. 2b). In 1981, 80% of the population still belonged to the year class 1979 (Table 1; Fig. 2c); O- and I-group animals made up only 18% of the total population, which is the reverse of the normal situation in open estuaries.

TABLE 2

Length and fresh weight of plaice and flounder from the dominant year class 1979 in September/October 1981 and December 1981, respectively. Number of fish is shown in brackets.

		Length in cm			*Weight in g*		
		mean	*s.d.*	*range*	*mean*	*s.d.*	*range*
Plaice							
♂♂	(39)	27.7	4.1	18.9-39.5	239.4	99.9	74-498
♀♀	(36)	29.7	4.5	19.6-38.7	326.9	167.9	70-725
Total	(75)	28.7	4.4	18.9-39.5	281.4	142.8	70-725
Flounder							
♂♂	(19)	26.4	3.1	18.0-31.2	215.6	78.5	49-358
♀♀	(21)	26.3	3.4	19.3-32.5	223.9	96.0	82-475
Total	(40)	26.3	3.2	18.0-32.5	220.0	87.3	49-475

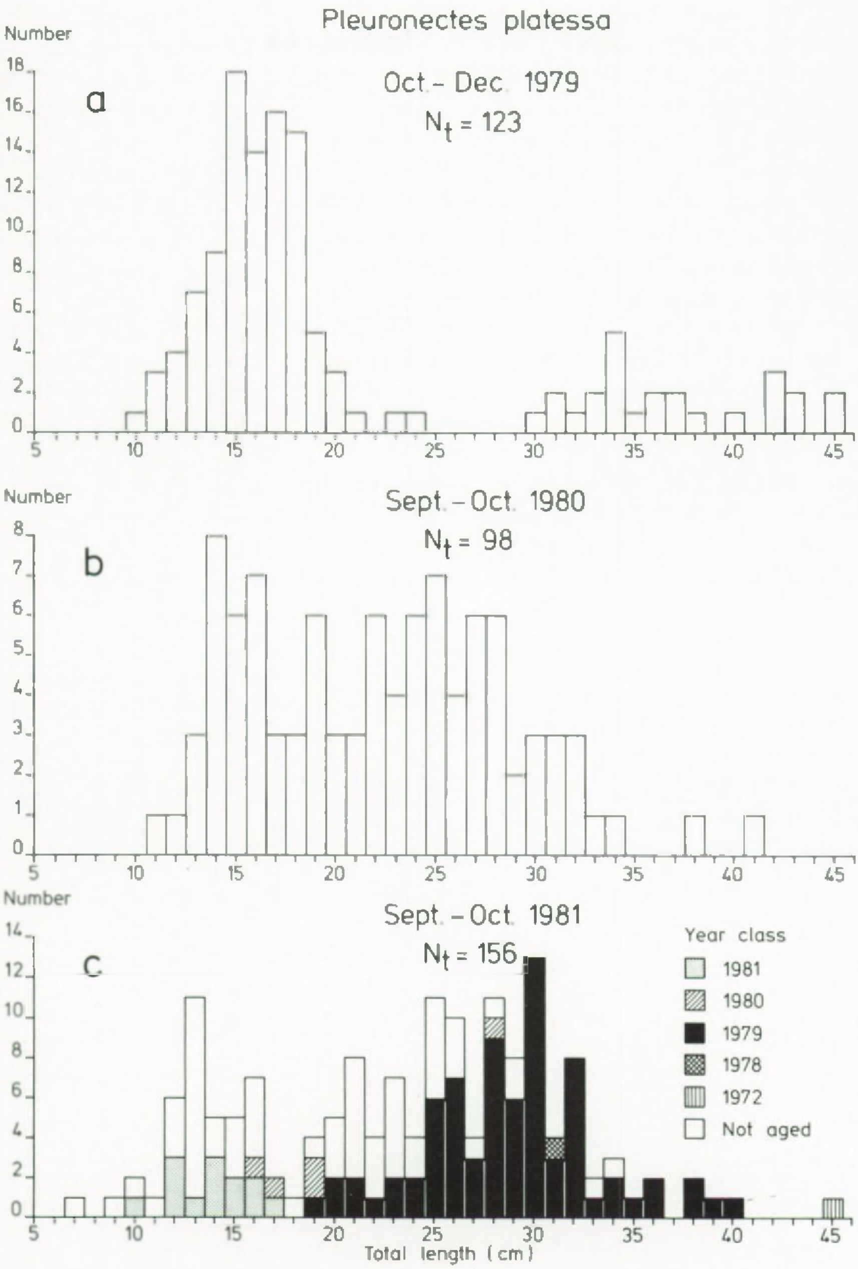


Fig. 2. Length-frequency distribution of plaice in: a. 1979, b. 1980 and c. 1981. In 1981, only part of the animals were aged.

The growth rate of year class 1979 plaice was high. In spring 1980 the average length was 14 cm and at the end of their third growing season, in autumn 1981, they measured on average 28.7 cm, females being about 2 cm longer than males (Table 2). After the first growing season the 1981 plaice had reached a mean length of 13.0 $\pm$ 2.0 cm and a mean fresh weight of 27.4 g. During May to November length growth could be described better by a second degree polynome than by the Von Bertalanffy expression (Fig. 3). (According to A. RIJNSDORP (personal communication) the larvae entered the lake at a length of about 12.1 mm before April 1, the date the sluice was closed).

The instantaneous growth rate (G) for plaice in 1980 and 1981 was 0.0035 and 0.0043, respectively (Table 3). In general, growth for comparable weight classes was better in 1981 than in 1980.

The male to female ratio in the catches was nearly one (1.02; N = 95).

In spite of the closed sluice, the estimated population size of plaice increased in 1980 and reached a maximum in August (Table 4). Until October, however, the area deeper than 15 m had not been fished. The 1981 data suggest that up to April the numbers in this deep area were

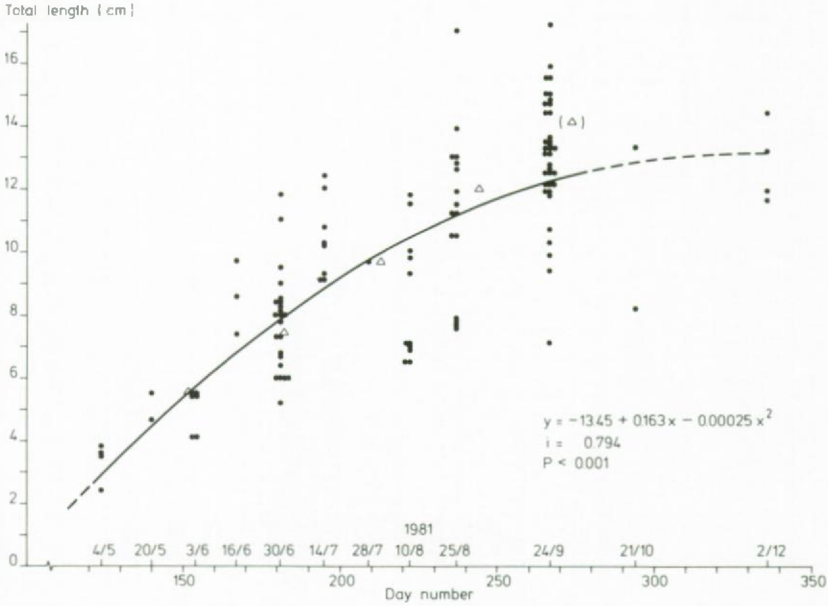


Fig. 3. Length growth of O-group plaice in 1981. Simulated monthly values according to FONDS (1979) are indicated (Δ).

TABLE 3

Computed mean length (L in cm), fresh weight (W in g) and instantaneous growth rate ($G = (\Delta t)^{-1} \ln W_2 \cdot W_1^{-1}$) of plaice and flounder, excluding year class 1981, during 1980 and 1981.

15-4-1980		*15-10-1980*			*Weight class*	*15-4-1981*		*15-10-1981*		
L	*W*	*L*	*W*	*G*		*L*	*W*	*L*	*W*	*G*
Plaice										
12.7	21.5	16.8	46.5	0.0042	Light	17.3	46.2	22.2	108.4	0.0047
17.8	55.4	21.4	98.7	0.0032	Medium	21.1	87.2	27.1	212.4	0.0049
23.0	113.6	27.6	219.0	0.0036	Heavy	26.4	180.8	32.0	367.9	0.0039
18.7	63.5	22.9	121.4	0.0035	all ind.	22.3	104.8	27.8	229.6	0.0043
Flounder										
19.9	92.9	24.5	155.6	0.0028	all ind.	24.0	144.1	26.6	216.3	0.0022

underestimated. Besides, gear efficiency is generally greater during the summer, particularly in August (see Chapter 4). Therefore the population size was estimated by averaging the May, June, July and September values, leading to a total of 1.3 (95% confidence interval 0.9-1.7) and 0.6 (0.5-0.8) million individuals for 1980 and 1981, respectively (Table 4). A very similar estimate of the 1981 stock size was obtained on the basis of three stratified random summer surveys (Table 5).

In both years the highest density of plaice was observed below the 5 m depth contour, while the fish almost completely avoided the littoral zone (Tables 4 and 5).

Only in September 1981 sufficient O-group plaice were caught to make a stock estimate. At that time about 0.2 million individuals were present. In order to calculate total annual food consumption, the same mortality rate $Z = (\Delta t)^{-1} \ln n_1 \cdot n_2^{-1}$ which ZIJLSTRA *et al.* (1982) obtained for juvenile Wadden Sea plaice of 0.023 d^{-1} for "settlers" (April-May) and 0.0049 d^{-1} for "post-settlers" (June-September) has been used. Thus their numbers should have decreased from about 1.4 million on April 1 to about 0.3 million on June 1.

3.1.2. FLOUNDER

At the end of 1979, the maximum length of flounders amounted to 34 cm (Fig. 4a). A distinct cohort of animals with a length of 6 to 15 cm can be distinguished in the size-frequency distribution. The flounders of this cohort had a mean length of ~ 11 cm and are presumed to belong to the year class 1979. Otolith samples from spring 1980 confirmed that 43% of the population belonged to the year class 1979 and 36% to 1978

TABLE 4

Absolute number (N) of plaice and flounder per month obtained by stratified sampling. The contribution of the extra hauls (below 15 m) to the mean number in the area deeper than 5 m is shown in brackets. An average population size, with its 95% confidence interval, has been assessed over May, June, July and September.

Period	*Plaice (N per stratum·10^3)*				*Flounder (N per stratum·10^3)*			
	0-2 m 43 km²	*2-5 m 27 km²*	*>5 m 38 km²*	*Total 108 km²*	*0-2 m 43 km²*	*2-5 m 27 km²*	*>5 m 38 km²*	*Total 108 km²*
1979								
Oct.	0	73	695	768	50	122	160	332
Nov.	0	24	160	184	43	149	790	982
Dec.	0	0	65	65	0	49	0	49
1980								
Jan.	0	0	30	30	43	24	190	257
Feb.	0	0	255	255	0	0	125	125
March	0	0	65	65	0	49	160	209
April	79	173	410	662	244	49	160	453
May	79	221	665	965	609	49	95	753
June	244	367	790	1401	487	97	95	679
July	43	294	950	1287	244	73	190	507
August	0	270	2405	2675	43	319	505	867
Sept.	43	367	1075	1485	43	197	540	780
Oct.	57	327	167	551	29	181	338	548
Nov.	0	62	255	317	0	22	160	182
			(597)	(659)			(137)	(159)
Dec.	0	41	380	421	0	167	315	482
			(707)	(748)			(490)	(657)
Total number assessed	≈ $1.3 \cdot 10^6$ ($0.9 - 1.7 \cdot 10^6$)				≈ $0.7 \cdot 10^6$ ($0.5 - 0.9 \cdot 10^6$)			
1981								
Jan.	0	0	125	125	79	41	125	245
			(163)	(163)			(110)	(230)
Feb.	0	208	380	588	0	41	255	296
			(650)	(858)			(380)	(421)
March	0	0	285	285	43	0	380	423
			(802)	(802)			(486)	(529)
April	0	103	160	263	43	41	30	114
			(695)	(798)			(106)	(190)
May	29	62	300	391	50	41	15	106
			(365)	(456)			(15)	(106)
June	36	262	486	784	72	41	118	231
			(524)	(822)			(118)	(231)
July	0	62	445	507	50	22	30	102
			(395)	(457)			(42)	(114)
Total number assessed	≈ $0.6 \cdot 10^6$ ($0.5 - 0.8 \cdot 10^6$)				≈ $0.2 \cdot 10^6$ ($0.1 - 0.2 \cdot 10^6$)			

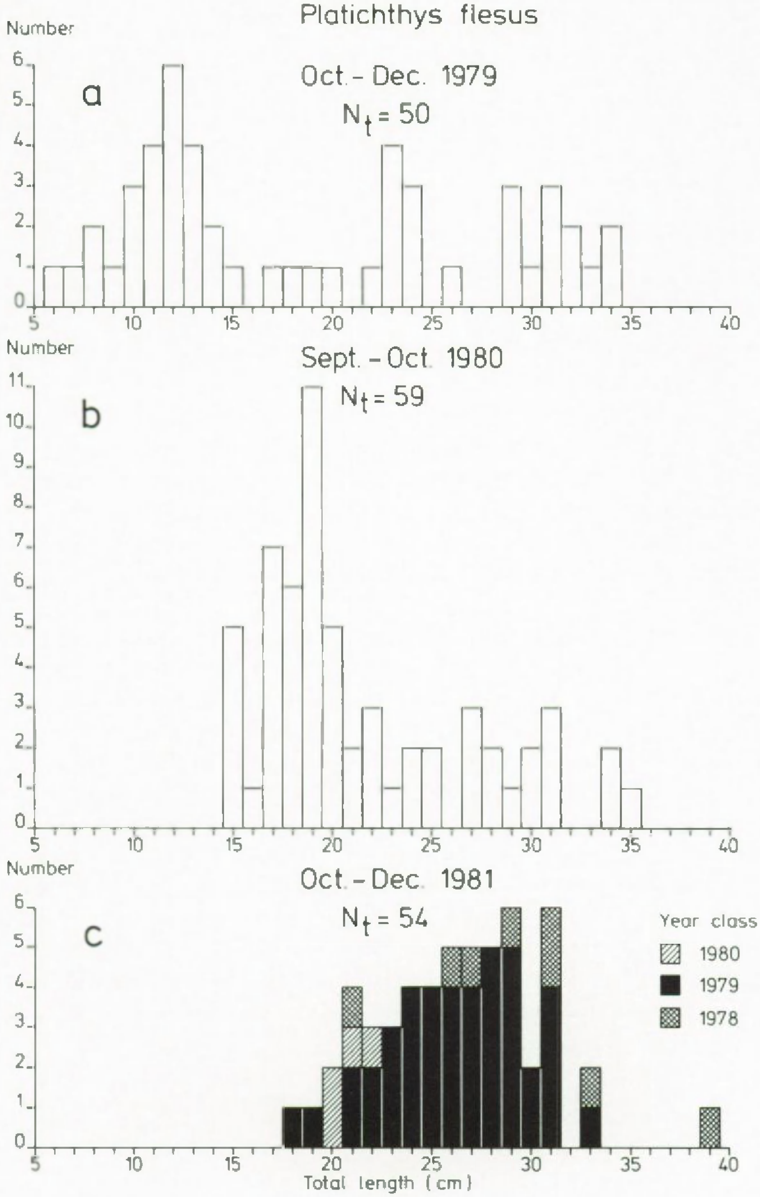


Fig. 4. Length-frequency distribution of flounder in: a. 1979, b. 1980 and c. 1981. The animals were also aged in 1981.

TABLE 5

Assessment of the absolute number (N) of plaice and flounder, excluding the O-group, based on the data of three stratified random surveys during July to September 1981. In brackets are the number of hauls.

Depth zone (m)	*Area (km²)*	*Plaice*		*Flounder*	
		N·10000 m⁻²	*95% Conf. limits*	*N·10000 m⁻²*	*95% Conf. limits*
>15	11 (28)	164.3	49.6-543.7	35.7	13.3-95.9
5-15	27 (58)	117.8	56.3-246.5	13.5	8.0-22.6
2- 5	27 (60)	38.2	19.6- 74.5	24.9	13.1-47.2
0- 2	43 (57)	0		3.6	2.7- 4.8
Total	108(203)	55.7	42.4- 73.2	14.7	11.4-18.8
Total number assessed		$\approx 0.6 \cdot 10^6$ $(0.5 - 0.8 \cdot 10^6)$		$\approx 0.2 \cdot 10^6$ $(0.1 - 0.2 \cdot 10^6)$	

(Table 1). At the end of 1980, the population was dominated (68%) by fish of 15 to 22 cm. Animals smaller than 15 cm were totally absent (Fig. 4b). During autumn 1981, 78% of the flounder population belonged to the year class 1979, now being fish of 18 to 33 cm long. Only 7% of the fish was one year old, while O-group animals were not observed at all (Table 1; Fig. 4c).

In spring 1980, the flounders of the 1979 year class were about 13.5 cm (VERNIJ, 1983) and at the end of 1981 they had reached an average length of 26.3 cm, males and females being about the same size (Table 2). Hence, growth rates in the year class 1979 flounder were exceptionally high. Total instantaneous growth rate within the flounder population was somewhat higher in 1980 than in 1981, *i.e.* 0.0028 and 0.0022, respectively (Table 3).

As with plaice, in 1980 the estimated number of flounders appeared to be low during spring and autumn, and high during summer (Table 4). However, during May to September the population size was fairly stable. During that period the stock of 1980 and 1981 was assessed at 0.7 (0.5-0.9) and 0.2 (0.1-0.2) million individuals, respectively (Tables 4 and 5). Contrary to plaice, flounder was more equally divided over the successive depth zones during summer.

3.2. DIET AND ANNUAL FOOD CONSUMPTION

3.2.1. PLAICE

Polychaetes strongly dominated in the diet of plaice in both years (Table 6). In 1980, lugworms *Arenicola marina* (whole animals as well as tail tips)

TABLE 6

Specified and total consumption by plaice (exluding year class 1981) and flounder in 1980 and 1981, in mg ash-free dry weight per m^2 per year. The data are means for the total surface of Lake Grevelingen (108 km^2).

Prey	*Plaice*				*Flounder*			
	1980		*1981*		*1980*		*1981*	
Polychaeta	923		806		416		232	
Arenicola marina	401	683	165	215	222	413	48	116
Arenicola tail tips	282		50		191		68	
Nephtys hombergii		140		150		–		24
Pectinaria koreni		33		6		–		–
Tharyx marioni		22		68		–		–
Nereidae		4		217		1		70
Capitellidae		2		70		1		4
Other Polychaeta		39		80		1		18
Mollusca	196		198		8		72	
Mya arenaria	–	57	35	40	–	5	30	40
Mya siphons	57		5		5		10	
Venerupis pullastra	89	90	51	71	1	1	–	4
Venerupis siphons	1		20		–		4	
Cerastoderma sp.	22	23	36	37	–	–	–	3
Cerastoderma siphons	1		1		–		3	
Hydrobia ulvae		14		5		–		–
Nassarius reticulatus		–		–		1		25
Other Mollusca		12		45		1		–
Crustacea	470		241		462		63	
Crangon crangon		304		213		282		51
Carcinus maenas		159		20		165		2
Praunus flexuosus		1		–		2		5
Other Crustacea		6		8		13		5
Other species	95		163		250		74	
Pomatoschistus sp.		28		57		207		23
Fish eggs		–		–		42		29
Actinothoe anguicoma		51		35		–		–
Rest		16		71		1		22
Total		1684		1408		1136		441

were favoured, while in 1981 the consumption of Nereidae (mainly *Nereis virens* and to a lesser extent *N. diversicolor*) and Capitellidae (mainly *Capitella capitata*) had strongly increased. *Nephtys hombergii* was important in both years. The contribution of bivalve spat and small molluscs remained constant. Regenerating parts of molluscs, such as siphons and mantle edges, were less important than in the case of polychaetes.

Crustaceans, particularly *Crangon crangon* and *Carcinus maenas*, were more heavily preyed upon in 1980 than in 1981.

Polychaetes and crustaceans were eaten throughout the whole year, while predation on molluscs was restricted to the summer period (Fig. 5). In plaice stomachs collected during the winter, more fish, mainly *Pomatoschistus minutus*, were found than in the rest of the year. However, as a consequence of the low metabolic rate in winter, overall fish consumption during the year was relatively small (Table 6). The abrupt depressions in the polychaete consumption during summer might be related to short periods of low oxygen concentrations near the bottom, during which polychaetes may have been inactive. During these interruptions the plaice shifted to molluscs, whose vulnerability to plaice is independent of their activity.

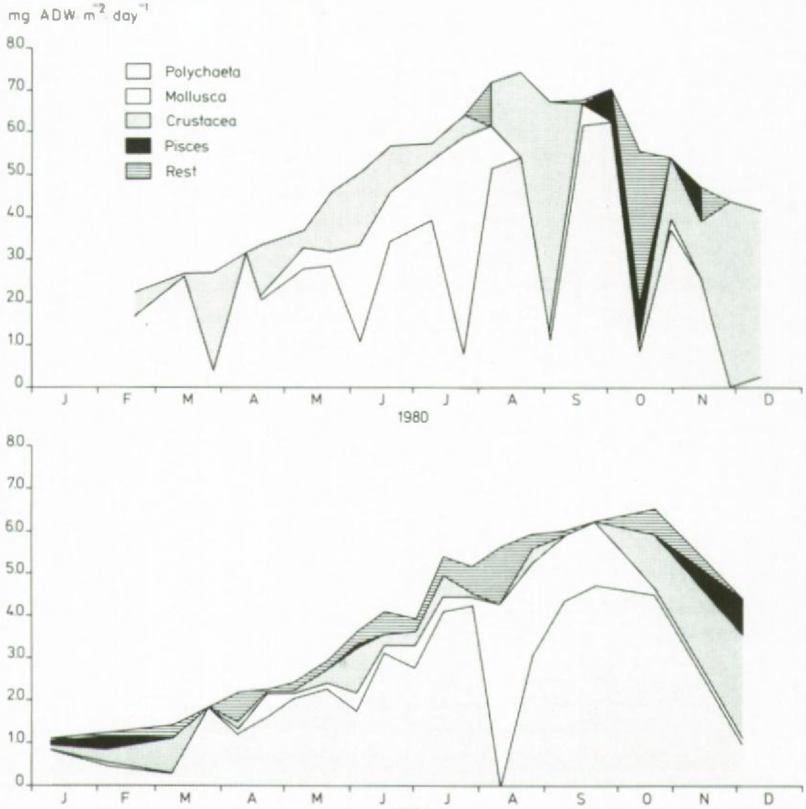


Fig. 5. Total daily food intake of plaice population in 1980 and 1981 (excluding year class 1981). The share of polychaetes, molluscs, crustaceans and fish is indicated.

In the 3 distinguished weight classes, the consumption of the "heavy" plaice was about 1.6 and 3 times that of the "medium" and "light" ones, respectively (Table 7). The same proportion can be found in the consumption of the main prey species. Only *Arenicola marina*, complete animals as well as tail tips, and *Pomatoschistus* sp. were eaten significantly more by larger plaice. On the other hand, the small polychaete *Tharyx marioni* was preyed upon much more by smaller plaice, while *Cerastoderma* sp. was particularly preferred by medium sized plaice. In their first half year of life the O-group plaice of 1981 fed predominantly on harpacticoid copepods, while those greater than about 6 cm fed upon small molluscs and polychaetes.

In spite of a halving of the older plaice stock, consumption in 1981 was hardly lower than in 1980, 1.41 (95% confidence interval 1.11-1.85) and 1.68 (1.18-2.19) g ADW$\cdot m^{-2} \cdot a^{-1}$, respectively (Table 6). With an estimated uptake of 0.06 g by the O-group, the consumption by the total stock in 1981 should have amounted to 1.47 g$\cdot m^{-2} \cdot a^{-1}$.

3.2.2. FLOUNDER

In both years, polychaetes and particularly *Arenicola marina* (including tail tips), were an important food source (Table 6). However, in 1981 the consumption of *Arenicola* decreased, whereas that of other polychaetes, mainly *Nereis virens* and *Nephtys hombergii*, increased. Molluscs were hardly eaten by flounders. In 1980 crustaceans were as important in the diet as polychaetes. *Crangon crangon* and small *Carcinus maenas* were par-

TABLE 7

Main prey species and total consumption by the three distinguished weight classes of plaice in 1981, in mg ash-free dry weight per m^2 per year.

Prey	*Weight class*			
	Light	*Medium*	*Heavy*	*Total*
Arenicola marina	1	22	192	215
Nephtys hombergii	43	41	66	150
Tharyx marioni	46	17	5	68
Nereidae	41	86	90	217
Capitellidae	6	32	32	70
Venerupis pullastra	10	23	38	71
Cerastoderma sp.	7	25	5	37
Crangon crangon	26	72	115	213
Pomatoschistus sp.	0	22	35	57
Rest	66	99	145	310
Total	246	439	723	1408

ticularly favoured. Consumption of crustaceans decreased considerably in 1981 and *C. maenas* was almost absent in flounder stomachs which may be attributed to an almost complete absence of small crabs (<20 mm maximum carapace width) in Lake Grevelingen in 1981 (LAMBECK & WESSEL, 1983). In plaice a similar reduction in crab consumption was observed (Table 6). During winter, flounder also consumed small fish, *i.e.* common goby *Pomatoschistus microps* and sand goby *P. minutus*. Egg clumps of the bull-rout *Myoxocephalus scorpius* were found in a number of stomachs.

Annual consumption of the flounder population during 1980 and 1981 is estimated at 1.14 (0.80-1.45) and 0.44 (0.21-0.44) g ADW$\cdot$m$^{-2}\cdot$a^{-1}, respectively (Table 6).

4. DISCUSSION

Although during the period March to October 1980 the saline Lake Grevelingen was an almost closed system, trawl catches of plaice and flounder increased in the course of the year to a maximum in August. The increase in spring and the decrease in autumn might be caused by a migration of fish from and towards the area deeper than 15 m which had not been fished until October 1980. When there is an aggregation of fish in deep water only during the colder part of the year, the surveys should give appropriate estimates of the population size during the rest of the year, as is indicated by the 1981 data.

Another bias might be introduced by seasonal differences in gear efficiency. Preliminary results of experimental work point to low efficiencies during spring and autumn, and high ones during summer. RILEY & CORLETT (1966) found a variable efficiency in catching juvenile plaice with a 4 m beam trawl increasing from 33% in March to 57% in August-September. In most studies, however, a constant gear efficiency is assumed, at least within the same size class (*e.g.* EDWARDS & STEELE, 1968; KUIPERS, 1975, 1977).

The activity of plaice will affect their ability to be caught. During 4 stratified random sampling surveys between July and September 1981 the total number of older plaice, estimated on basis of a gear efficiency of 20%, was 0.60, 1.59, 0.68 and 0.52 million individuals, respectively. During the second survey on 10 and 11 August, which followed a period of several sunny and windless days, nearly all plaice had empty stomachs. This might indicate that oxygen concentrations have been very low near the bottom in the deeper parts of the lake, as was also demonstrated by LINDEBOOM & SANDEE (1984) under similar weather conditions in 1982. Lack of oxygen is likely to result in a passive (non-feeding) and more epibenthic way of life of the fish. Because of the 2 to

3 times larger catches during that survey, these data have been excluded from the stock assessment.

Although larger flounders were regularly observed in shallow water, few were actually caught. This points to a low efficiency of the 1.9 m beam trawl for catching larger specimens. Hence, in the 0 to 2 m depth zone the number of flounders might have been underestimated.

Based on the Wadden Sea data of ZIJLSTRA *et al.* (1982), a monthly mortality rate of 15% for O-group plaice during June to September was assumed for the Grevelingen which is rather low in comparison with mortalities observed in British bays ranging from 17 to 70% with a mean value of 45% (RILEY & CORLETT, 1966; MACER, 1967; EDWARDS & STEELE, 1968; STEELE & EDWARDS, 1970; BANNISTER *et al.*, 1974; POXTON *et al.*, 1982). High mortality rates are attributed almost entirely to predators (KUIPERS, 1977). In Lake Grevelingen few piscivorous fish are present. In 1980 and 1981 no remains of young plaice were found in the approximately 1000 stomachs of plaice and flounder examined. Also in the less frequently sampled stomachs of dab *Limanda limanda*, bull-rout *Myoxocephalus scorpius*, eel *Anguilla anguilla*, turbot *Scophthalmus maximus* and brill *S. rhombus* no remains of O-group plaice were traced. On the other hand, during July to October about 500 to 800 cormorants *Phalacrocorax carbo* are foraging on the lake which could eat small flatfish.

Brown shrimps *Crangon crangon* are known to prey on young plaice (<30 mm) and even the shore crab *Carcinus maenas* is a potential predator (BERGMAN *et al.*, 1976). Crabs are rather common in the lake, while shrimps are less abundant, compared to the Wadden Sea (R.D.H. LAMBECK, personal communication).

Compared to other areas the growth of O-group Grevelingen plaice is very fast. On the Balgzand (Dutch Wadden Sea) the mean length at the end of the first growing season during 1972 to 1975 varied from 8 to 11 cm (KUIPERS, 1977). Values ranged from 6 to 8 cm in British bays (MACER, 1967; STEELE & EDWARDS, 1970). Only the juveniles off the Belgian coast (9 to 12 cm) approach the size of those in the Grevelingen (DE CLERCK, 1978, 1980, 1981).

ZIJLSTRA *et al.* (1982) demonstrated that the observed growth of O-group plaice between June and September in the Dutch Wadden Sea and in several British bays could be simulated effectively by the experimental model of FONDS (1979) in which under an unlimited food supply growth appeared to be a function of the ambient water temperature. In Lake Grevelingen, where summer temperatures are high (up to 20°C), the data for year class 1981 fit this model very well (Fig. 3). This also implies that in the lake, growth must be regarded as non-food-limited.

Growth before June is presumably favoured by the lower densities and a higher water temperature as compared to the western Wadden Sea (*cf.* ZIJLSTRA *et al.*, 1982). In addition, only the earliest arriving larvae could have succeeded in entering the lake before the closing of the sluice on April 1, which might have given the Grevelingen O-group a length advantage.

Growth in older plaice was also exceptionally fast. In October 1981, males and females of the year class 1979 caught in the North Sea along the Dutch coast had a mean length of 25.1 and 25.2 cm, respectively (A. RIJNSDORP, personal communication). This is 2.6 and 4.5 cm shorter than Grevelingen plaice of the same year class at the same time.

In the similarly enclosed Lake Veere, VAAS (1970) also observed a fast growth in O- and I-group plaice. As fish grew older, the rate of growth there, however, slowed down and the size at the same age became less than plaice found in the Southern Bight.

The population size of plaice and flounder in 1980 and 1981 cannot be compared directly to previous years because no estimates of stock size have been published so far. Still, based on catch data from STEINMETZ & SLOTHOUWER (1979) and VAAS (unpublished), an attempt was made to reconstruct the size of the plaice stock during 1971 to 1978 (Fig. 6). In both data sets only waters deeper than 5 m have been fished with a 3 m beam trawl without any tickler chain. If it is assumed that ever since autumn 1972 all plaice stayed in the area deeper than 5 m (38 km^2) and that the gear efficiency was 10%, the extrapolated population size in September 1971, the year of enclosure, should have amounted to about 14 million fish (Fig. 6) of which according to STEINMETZ & SLOTHOUWER (1979) 75% belonged to the year class 1971. This number, implying an average density of 0.13 individuals·m^{-2}, may be regarded as an estimate of the former estuarine stock. Although the present density might be raised to some extent by a more appropriate sluice management, *e.g.* when focussed on the immigration of larvae and one year old fish during February to May and on the retention of the fish in autumn and early winter, total stock size can only reach a fraction of the estuarine stock.

From the data (Fig. 6) an overall mortality rate *Z* of 0.0011 per day for older plaice has been calculated. Assuming a similar mortality, the "loss" of plaice within one year would lie within the range of the 95% confidence limits of the estimated population numbers for both years. Hence, mortality was ignored in the calculations which implies that the daily food intake of the plaice population (Fig. 5) has been underestimated somewhat during spring and overestimated during autumn.

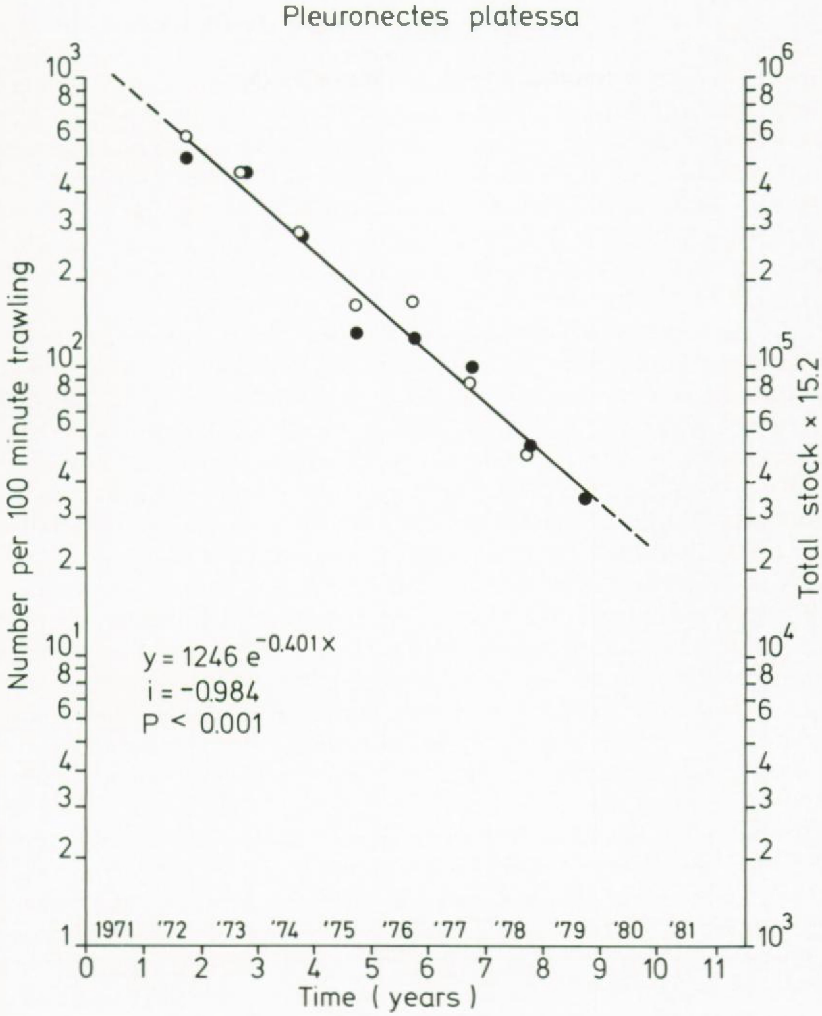


Fig. 6. Number of plaice caught per 100 minute trawling interval in the deeper parts (>5 m) of Lake Grevelingen during 1972-1979, based on STEINMETZ & SLOTHOUWER, 1979 (○) and unpublished data of the Delta Institute (●). By means of the computed regression, the stock size over the successive years has been reconstructed (see context).

In the former Grevelingen estuary, WOLFF *et al.* (1981) observed flounder feeding in the upper as well as the lower parts of the intertidal flats while plaice were seen only in the latter area. They considered this difference as a mechanism to reduce competition for food. Even in the stagnant lake a similar difference in distribution exists. The food competition hypothesis seems to be confirmed by the almost similar food spectra of plaice and flounder in both years. According to R.H.D. LAMBECK (personal communication) the average biomass of *Arenicola marina*, *Nephtys hombergii* and Nereidae amounts to about 3 g, 0.5 g and 0.3 g ADW·m^{-2}, respectively, which exceeds the assessed annual consumption of plaice and flounder populations 2 to 10 times. The increase in density of *Nereis virens* in the lake coincides with a much higher consumption in 1981 than in 1980. On the other hand, the lack of bivalve spat in both years may be responsible for the relatively low mollusc predation.

As the water is usually well mixed in the lake, a salinity-determined distribution of flounder as assumed by RILEY *et al.* (1981) does not hold.

Considering the food and feeding habits of flatfish, DE GROOT (1971) classified plaice as a polychaete-mollusc feeder and flounder as a crustacean feeder. This is more or less confirmed by our data, although in Lake Grevelingen the plaice consumed slightly more crustaceans than molluscs and flounder also ate a considerable amount of polychaetes, particularly in 1981. On the Balgzand area, DE VLAS (1979) also observed that polychaetes (like *Arenicola marina, Pygospio elegans, Tharyx marioni, Nephtys hombergii* and *Heteromastus filiformes*) formed the main part of the plaice (57%) and flounder (54%) diets, percentages that are very similar to those in the Grevelingen. In Red Wharf Bay (Wales), I-group plaice consumed mainly polychaetes (*e.g. Nephtys* sp. and *Phyllodoce* sp.) and to a lesser extent crustaceans (predominantly the amphipod *Ampelisca* sp.) and molluscs (MACER, 1967). On the other hand, plaice in Lake Veere fed primarily on *Corophium* sp., while bivalves like *Mya arenaria* and *Cerastoderma lamarcki* and polychaetes such as *Heteromastus filiformes* and Nereidae were of less importance (VAAS, 1970). In addition, *Corophium volutator* was the main prey item for flounder on the upper mudflats of the Ythan estuary, while small polychaetes and oligochaetes were eaten on the softer mudflats in the middle region. *Nereis diversicolor* and *Carcinus maenas* were eaten on the mussel beds, while at the mouth of the estuary older flounder preyed upon shoals of clupeids (SUMMERS, 1980). In general, however, there may also be a considerable differentiation in diet from one year to another, presumably due to the availability of the prey species. In Gullmarsvik bay (Sweden), PIHL (1982) observed I- to IV-group flounder to feed in 1980 on polychaetes (*e.g.* Nereidae) and in 1979 mainly on *Mya arenaria, Mytilus edulis* and *Cerastoderma* sp., coinciding with a 10 to 100 times higher mollusc spat density in 1979 than in 1980.

With respect to annual food consumption by plaice and flounder populations, few comparable data are available. At the Balgzand area, DE VLAS (1979) assessed an average food intake for plaice and flounder of 5.6 and 0.9 g ADW$\cdot$m$^{-2}\cdot$a^{-1}, respectively. According to WOLFF *et al.* (1981), II-group plaice consumed about 0.5 to 1.5 g ADW$\cdot$m^{-2} on the intertidal flats of the former Grevelingen estuary from March to May, for which a 3 to 4 times higher annual consumption can be deduced. In Gullmarsvik bay the consumption by the flounder population amounted to about 0.5 g fresh weight$\cdot$m$^{-2}\cdot$a^{-1}, which will be nearly 0.09 g ADW (PIHL, 1982).

5. SUMMARY

Within the scope of a carbon budget study in the 108 km^2 saline Lake Grevelingen, investigations on the plaice and flounder populations were made during October 1979 to December 1981. Both populations were dominated by the 1979 year class that presumably entered the lake as larvae in the year the Brouwerssluice, which opens to the North Sea, was operative the whole year round.

Due to high summer temperatures in the lake, juvenile plaice (year class 1981) attained a mean length of 13.0 cm and a fresh weight of 27.4 g at the end of their first growing season. At the end of their third year, year class 1979 males measured on average 27.7 cm and females 29.7 cm, which is about 3.5 cm more than plaice of the same age in the North Sea. Flounder reached a mean length of 26.3 cm in 3 years.

Total stock of plaice, excluding year class 1981, was estimated at an average of 1.3 million over 1980 and at 0.6 million fish over 1981. For flounder these figures were 0.7 million and 0.2 million fish, respectively. In September 1981 the number of O-group plaice was assessed at about 0.2 million individuals.

About 56% of the plaice food consisted of polychaetes, mainly consisting of in 1980 *Arenicola marina* (41%) and in 1981 *A. marina* (15%), Nereidae (15%) and *Nephtys hombergii* (11%). Larger plaice consumed significantly more *Arenicola* and less *Tharyx marioni* than smaller ones. Polychaetes and crustaceans were eaten the whole year round while the consumption of molluscs was restricted to the summer period and that of fish to autumn and winter. In 1980 the flounder population preyed predominantly upon crustaceans (41%) and polychaetes (37%), with *Arenicola marina* (36%) and *Crangon crangon* (25%) as the most important species. In 1981 relatively more polychaetes (53%) and less crustaceans (14%) were eaten.

Total consumption of plaice population, excluding year class 1981, in 1980 and 1981 was estimated at 1.68 g and 1.41 g ADW$\cdot$m$^{-2}\cdot$a^{-1}. Annual consumption of O-group 1981 plaice was assessed at about 0.06 g ADW. The corresponding consumption of the flounder population was 1.14 g and 0.44 ADW, respectively.

6. REFERENCES

BANNISTER, R.C.A., D. HARDING & S.J. LOCKWOOD, 1974. Larval mortality and subsequent year-class strength in the plaice (*Pleuronectes platessa* L.). In: J.H.S. BLAXTER. The early life history of fish. Springer-Verlag, Berlin: 21-37.

BERGMAN, M.J.N., B.R. KUIPERS, P.J. SPLIETHOFF & H.W. VAN DER VEER, 1976. Garnalen en krabben als mogelijke predatoren van O-jarige schol op het Balgzand.—Visserij **29:** 432-438.

CLERCK, R. DE, 1978. Growth of juvenile soles, plaice, and dab off the Belgian coast.—Annls biol., Copenh. **33:** 161-163.

——, 1980. Growth of juvenile sole, plaice, and dab off the Belgian coast in 1977 and 1978.—Annls biol., Copenh. **35:** 225-229.

——, 1981. Growth of O-group sole, plaice and dab off the Belgian coast in 1979.—Annls biol., Copenh. **36:** 175-176.

COCHRAN, W.G., 1963. Sampling techniques. Wiley, London: 1-413.

DOORNBOS, G., 1982. Changes in the fish fauna of the former Grevelingen estuary, before and after the closure in 1971.—Hydrobiol. Bull. **16:** 279-283.

EDWARDS, R. & J.H. STEELE, 1968. The ecology of O-group plaice and common dabs at Loch Ewe. I. Population and food.—J. exp. mar. Biol. Ecol. **2:** 215-238.

FONDS, M, 1976. The influence of temperature and salinity on growth of young sole, *Solea solea* L. In: G. PERSOONE & E. JASPERS. Proceedings of the 10th European Symposium on Marine Biology, 1. Universa Press, Wetteren: 109-125.

——, 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In: E. NAYLOR & R.G. HARTNOLL, Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford: 151-156.

GROOT, S.J. DE, 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes).—Neth. J. Sea Res. **5:** 121-196.

KUIPERS, B.R., 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*).—Neth. J Sea Res. **9:** 69-85.

——, 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea.—Neth. J. Sea Res. **11:** 56-91.

LAMBECK, R.D.H. & E.G.J. WESSEL, 1983. A survey of the score crab (*Carcinus maenas* L.) in Lake Grevelingen.—Verh. K. ned. Akad. Wet., Afd. Natuurkunde (2) **81:** 29-31.

LINDEBOOM, H.J. & A.J.J. SANDEE, 1984. The effect of coastal engineering projects on microgradients and mineralization reactions in sediments.—Wat. Sci. Tech. **16:** 87-94.

MACER, C.T., 1967. The food web in Red Wharf Bay (North Wales) with particular reference to young plaice (*Pleuronectes platessa*).—Helgoländer wiss. Meeresunters. **15:** 560-573.

NIENHUIS, P.H., 1978a. An ecosystem study in Lake Grevelingen, a former estuary in the SW Netherlands.—Kieler Meeresforsch. (Sonderheft) **4:** 247-255.

——, 1978b. Lake Grevelingen: a case study of ecosystem changes in a closed estuary.—Hydrobiol. Bull. **12:** 246-259.

PIHL, L., 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast.—Neth. J. Sea Res. **15:** 419-432.

POXTON, M.G., A. ELEFTHERIOU & A.D. MCINTYRE, 1982. The population dynamics of O-group flatfish on nursery grounds in the Clyde Sea area.—Estuar. coast. Shelf Sci. **14:** 265-282.

RILEY, J.D. & J. CORLETT, 1966. The numbers of O-group plaice in port Erin Bay, 1964-66.—Rep. mar. biol. Stn Port Erin **78:** 51-56.

RILEY, J.D., D.J. SYMONDS & L. WOOLNER, 1981. On the factors influencing the distribution of O-group demersal fish in coastal waters.—Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer **178:** 223-228.

SAMPFORD, M.R., 1962. An introduction to sampling theory. Oliver and Boyd, London: 1-292.

STEELE, J.H. & R.C. EDWARDS, 1970. The ecology of O-group plaice and common dabs in Loch Ewe. IV. Dynamics of the plaice and dab population.—J. exp. mar. Biol. Ecol. **4:** 174-187.

STEINMETZ, B. & D. SLOTHOUWER, 1979. De betekenis van de Grevelingen voor de sportvisserij. Visserijkundige waarnemingen in de jaren 1971-1977. Directie van de Visserijen, Den Haag: 1-101 (unpublished report).

——, 1980. Fishery experience with the stagnant salt Lake Grevelingen after its closure. In: J.H. GROVER. Allocation of fishery resources. Proc. Techn. Consult. Alloc. Fish. Resourc., Vichy, France. United Nations Food and Agriculture Organization: 396-402.

SUMMERS, R.W., 1980. The diet and feeding behaviour of the flounder *Platichthys flesus* (L.) in the Ythan estuary, Aberdeenshire, Scotland.—Estuar. coast. mar. Sci. **11:** 217-232.

VAAS, K.F, 1970. Studies on the fish fauna of the newly created lake near Veere, with special emphasis on the plaice (*Pleuronectes platessa*).—Neth. J. Sea Res. **5:** 50-95.

——, 1979. Studies on the fish fauna of an estuary in the S.W. Netherlands, before and after its change into the stagnant, saline, Lake Grevelingen.—Hydrobiol. Bull. **13:** 177-188.

VERNIJ, H., 1983. Oriënterend onderzoek naar de leeftijdsopbouw en het voedsel van schol (*Pleuronectes platessa* L.) en bot (*Platichthys flesus* (L.)) in het Grevelingenmeer na het openen van het doorlaatwerk in de Brouwersdam. Studentenverslag Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, D9-1983: 1-42 (unpublished report).

VLAS, J. DE, 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey.—Neth. J. Sea Res. **13:** 117-153.

WINBERG, G.G., 1956. Rate of metabolism and food requirements of fishes.—Fish. Res. Bd Can. Transl. Ser. **194:** 1-202.

WOLFF, W.J., M.A. MANDOS & A.J.J. SANDEE, 1981. Tidal migration of plaice and flounders as a feeding strategy. In: N.V. JONES & W.J. WOLFF. Feeding and survival strategies of estuarine organisms. Plenum Publ., New York, London: 159-171.

ZIJLSTRA, J.J., R. DAPPER & J.IJ. WITTE, 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea.—Neth. J. Sea Res. **15:** 250-272.

CHAPTER
HOOFDSTUK

4

Delta Institute for Hydrobiological Research
Progress Report 1982: 37-39 (1983)

FAST GROWTH OF 0-GROUP PLAICE (*Pleuronectes platessa* L.) IN LAKE GREVELINGEN

by

G. DOORNBOS, R.H. BOGAARDS
and
P. DE KOEIJER

From an economical point of view the growth rate of commercial fish species is very important.

In The Netherlands the statutory minimum size of catchable plaice *Pleuronectes platessa* is 25 cm,* reached in the North Sea in 3-4 years. Factors as *e.g.* density, food supply, diseases, water temperature etc. can influence growth rate, which may explain the remarkable differences in average length reached by juvenile plaice at the end of their first growing season (L_I) in the various nursery areas in n.w. Europe (Table 5).

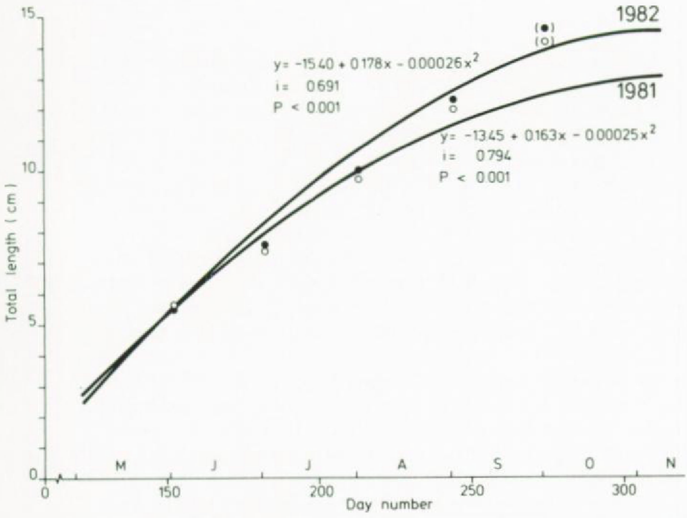


Fig. 18. Growth of 0-group plaice, year classes 1981 and 1982, in Lake Grevelingen compared to the simulated increase in mean length according to Fonds (1979) (0 = 1981; ● = 1982).

* 27 cm since 1984

Table 5. Differences in mean total body length (L_I) of juvenile plaice at the end of their first growing season in various nursery areas and years

Area	Year	Mean L_I (in cm)	Reference
Red Wharf Bay	1963	8	Macer, 1967
" " "	1964	8	" "
" " "	1965	6	" "
Loch Ewe	1965	7	Steele and Edwards, 1970
" "	1966	7	" " " "
" "	1967	6	" " " "
" "	1968	7	" " " "
Balgzand	1972	8	Kuipers, 1977
"	1973	10	" "
"	1974	10	" "
"	1975	11	" "
Belgian coast	1976	12	De Clerck, 1978
" "	1977	9	De Clerck, 1980
" "	1978	9	" " "
" "	1979	12	De Clerck, 1981

On the Balgzand (western Waddenzee) Zijlstra *et al.* (1982) observed a negative correlation between the abundance of post-larvae during settling (mainly in April and May) and the length of the fish on June 1st. However, after that date, monthly growth (Δ L) of juvenile plaice in the field could be described as a linear function of body length (L in cm) and ambient water temperature (T in ^{o}C), according to the emperical model of Fonds (1979): $\Delta L = 0.12\,T + 0.05\,L - 0.4$. So during summer period growth was neither density-dependent nor limited by feeding conditions.

The L_I values in Lake Grevelingen for the year classes 1981 and 1982, respectively 13.0 cm (range 7-17 cm) and 14.5 cm (range 8-20 cm), appeared to be the highest known for natural waters in n.w. Europe (Table 5). Only under artificial growing conditions, *e.g.* in sea water mixed with warm effluent of the Hunterston nuclear power plant (Scotland), the L_I of plaice became somewhat larger, namely 15.3 cm (Bardach *et al.*, 1972).

Over the period May to November growth of 0-group Lake Grevelingen plaice could be described better by a second degree polynome than by the von Bertalanffy expression (Fig. 18). From June through September the linear function of Fonds fits almost just as well. This implies that the fast growth of juvenile plaice is primarily a result of the high water temperatures in the lake during summer time (up to 20^{o}C), which are a consequence of the enclosing of the former Grevelingen estuary in 1971.

The increase in weight is more spectacular than the length growth, because of the length-weight relationship $W = a\,L^{b}$, in which the exponent b has a value close to 3. At the end of their first growing season 0-group Lake Grevelingen plaice of year classes 1981 and 1982 had reached a mean fresh weight of 27.4 and 37.3 g, respectively. Compared to the Wadden Sea the Grevelingen plaice gained weight approximately three times as fast.

References

Bardach, J.E., J.H. Ryther and W.O. McLarney - 1972. Aquaculture. The farming and husbandry of freshwater and marine organisms. Wiley-Interscience, New York, 868 pp.

De Clerck, R. - 1978. Growth of juvenile soles, plaice, and dab off the Belgian coast. Ann. Biol., Copenh. 33, 161-163.

De Clerck, R. - 1980. Growth of juvenile sole, plaice and dab off the Belgian coast in 1977 and 1978. Ann. Biol., Copenh. 35, 225-229.

De Clerck, R. - 1981. Growth of 0-group sole, plaice, and dab off the Belgian coast in 1979. Ann. Biol., Copenh. 36, 175-176.

Fonds, M. - 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In: E. Naylor and R.G. Hartnoll (eds.). Cyclic phenomena in marine plants and animals. Proc. 13th Eur. Mar. Biol. Symp., Isle of Man, Great-Britain. Pergamon Press, Oxford, pp. 151-156.

Kuipers, B.R. - 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. Neth. J. Sea Res. 11, 1, 56-91.

Macer, C.T. - 1967. The food web in Red Wharf Bay (North Wales) with particular reference to young plaice (*Pleuronectes platessa*). Helgoländer wiss. Meeresunters. 15, 1/4, 560-573.

Steele, J.H. and R.C. Edwards - 1970. The ecology of 0-group plaice and common dabs in Loch Ewe. IV. Dynamics of the plaice and dab population. J. Exp. Mar. Biol. Ecol. 4, 174-187.

Zijlstra, J.J., R. Dapper and J.Y. Witte - 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea Res. 15, 2, 250-272.

CHAPTER HOOFDSTUK 5

Netherlands Journal of Sea Research
21(1): 45-74 (1987)

DENSITY, GROWTH AND ANNUAL FOOD CONSUMPTION OF GOBIID FISH IN THE SALINE LAKE GREVELINGEN, THE NETHERLANDS*

G. DOORNBOS and F. TWISK

Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA Yerseke, The Netherlands

ABSTRACT

Within the scope of a study of the carbon budget of the 108 km² saline Lake Grevelingen, investigations were made on density, mortality, growth and food consumption of the main gobiid fish during the period 1980 to 1982.

In August 1980 the O-group of *Pomatoschistus minutus* was estimated at 424 million individuals (on average 3.9 fishes per m²) with a biomass of 203 tons FW. In 1981 and 1982 peak numbers were less high. O-group *P. microps* accounted for 282 million individuals (2.6 fishes per m²) and 133 tons FW in September 1981. By far the highest density was found in the 0 to 0.6 m zone, 15 common gobies per m² (7 g FW·m^{-2}). With approximately 5.1 million individuals (13 tons FW) *Gobius niger* was most abundant in 1982.

For adult *G. niger* a monthly mortality of 27% was estimated. Mortality rates in *P. minutus* and *P. microps* were found to be fairly constant over the year. The estimated rates of annual mortality of 99.9% (~46% per month) and 99.996% (~57% per month), respectively, appear to be much higher than recorded for estuarine populations. Approximately 60% of the decline in numbers of demersal gobiid fish could be accounted for by the predation of two species of flatfish and two species of piscivorous birds.

Young of the year of over 20 mm total length of both species were first caught in June. At the end of the first growing season, the average length and weight of *P. microps* was 39 mm and 0.6 g FW. In their second year they attained an average size of 51 mm. In O-group *P. minutus*, the 1980 and 1981 year classes reached an average length of 45 mm and 57 mm, respectively. In their second year, however, the difference disappeared and the mean length in both classes approximated 62 mm. Juvenile *G. niger* were first caught in August at a length of approximately 3.5 cm. They attained an average size of 4 to 5 cm in the first year, 8 to 8.5 cm in the second and 11 to 12.5 cm in the third year.

The maximum production of *P. minutus* and *P. microps*, although reached in alternate years, amounted to 1.1 g and 0.8 g ADW·m^{-2}·a^{-1}, respectively, of which 92 to 98% was realized before the moment the maximum numbers (of individuals larger than 20 mm) were actually caught (August/September).

In 1980, the diets of *P. microps* and *P. minutus* up to a size of approximately 40 mm consisted largely of copepods. With increasing length, they switched to larger epibenthic crustaceans. Annual food consumption for the 1980 *P. minutus* year class and 1981 *P. microps* year class was estimated at 1.95 g and 1.6 g ADW·m^{-2}, respectively. The former species derived 91% of its annual food demands from copepods, and in the latter it was even 95%.

1. INTRODUCTION

The Grevelingen estuary was enclosed in 1971. Within the scope of investigations on the carbon budget of the Lake Grevelingen ecosystem (*cf.* NIENHUIS, 1978a, 1978b), a 4-year study on the quantitative importance of the fish fauna started at the end of 1979. Reports on various aspects have been published elsewhere (*e.g.* DOORNBOS, 1981, 1982, 1984, 1985; DOORNBOS & TWISK, 1984). The present study assesses the role of the main gobiid fish species in the food web of the lake on the basis of density, growth and annual food consumption.

Communication no. 360 of the Delta Institute for Hydrobiological Research, Yerseke, The Netherlands

In the stagnant and saline lake, 5 species of Gobiidae have been recorded so far. The transparent goby *Aphia minuta* and the painted goby *Pomatoschistus pictus* have been observed only incidentally, the latter only since 1979 (DOORNBOS, 1981). After the first record in 1976, the black goby *Gobius niger* has increased strongly. Dominant species, however, are the common goby *P. microps* and the sand goby *P. minutus*. These fishes propagate successfully in the lake (VAAS, 1979; DOORNBOS, 1982) and constitute an important food source for fish-eating birds and flatfish (DOORNBOS, 1984; DOORNBOS & TWISK, 1984).

Acknowledgements.—This study is part of the ZOWEC project (saline water ecology) financed by the former Delta Dienst of Rijkswaterstaat. We are much indebted to those who assisted in the field and in the laboratory, as well as to those who gave valuable advice and support. We especially want to thank: W.J.L. Robër and P. de Koeijer of the research vessel "Maris Stella", and Dr. A.G. Vlasblom and J.J. Guerand of the biomathematical department. R.H. Bogaards assisted in the field, while J.W. Francke worked out part of the data. Mrs M.J. van Leerdam-de Dreu did the typing and A.A. Bolsius made the final drawings.

The research on the food of *P. microps* and *P. minutus*, and on the fish fauna in the littoral was done by the students A.K. Glazenburg, V. Erenst and P.J.F. de Graaf, respectively. The procedure for estimating food consumption resulted from discussions with Dr. M. Fonds. R.H.D. Lambeck, and Dr. N. Daan gave comments on the first draft of the manuscript.

2. STUDY AREA, MATERIAL AND METHODS

2.1. STUDY AREA

Lake Grevelingen has a surface area of 108 km^2 and a mean water depth of 5.3 m, about 40% of the area being less than 2 m deep. Maximum water depths of 48 m are found in the former tidal gullies (Fig. 1). In the newly created lake, the chlorinity declined steadily, from more than 17 ‰ Cl$^-$ in 1971 to less than 13 ‰ Cl$^-$ in 1978. From December 1978 onwards, the chloride concentration was stabilized at approximately 16 ‰ Cl$^-$ by exchanging lake water against North Sea water during winter (mid-October through February). Only in 1979 was the Brouwerssluice (capacity 100 to 140 m^3.s^{-1}) operated the whole year round. Further details on hydrography and environmental parameters are given by BANNINK *et al.* (1984).

2.2. SAMPLING

For 3 years (1980-1982), trawling surveys in the deeper parts (>2 m) of the lake were carried out by the 18 m m.v. "Maris Stella" equipped with a 3 m beam trawl (6 x 6 mm mesh size in the cod-end) and covering, at standard speed, a swept area of 250 m^2 per minute. In the littoral zone a KUIPERS' (1975) 1.9 m beam trawl (5 x 5 mm mesh size), which covers 197 m^2 per minute, was used from the 6½ m boat "Riekus" with outboard motor. The foot rope of both nets was made heavier with an iron chain.

During 1980 and 1981, sampling trips were undertaken biweekly (weather permitting), while in 1982 only 5 surveys were made. As both in 1978 and 1979, stocks of eelgrass (*Zostera marina*), *Chaetomorpha* sp. and mussels (*Mytilus edulis*) had been very abundant, 41 to 48 fixed stations on fishable positions, spread over 3 depth strata: 0 to 2 m (43 km^2), 2 to 5 m (27 km^2) and deeper than 5 m (38 km^2), were selected for the surveys. However, up to October 1980, the area deeper than 20 m (3 km^2) was not surveyed, while during the period November 1980 through June 1981 this was done only incidentally (Fig. 1). Also because of the eelgrass and mussels, hauls of only 2 and 2½ minutes were made with the 3 m and 1.9 m trawl, respectively.

From July 1981 onwards, a strong decline in eelgrass and mussels, however, allowed us to change towards a stratified random sampling scheme, which is more satisfactory from a statistical point of view. For that purpose, a 500 x 500 m^2 grid was drawn on the map of Lake Grevelingen. The more favourable field condition also allowed us to double the number of the hauls as well as the haul duration. Moreover, the gear efficiency was improved by using one tickler chain in front of the foot rope. At the same time, the deep stratum was split up into a 5 to 20 m (35 km^2) and a deeper than 20 m (3 km^2) zone, since evidence had been obtained that part of the fish accumulated in the deepest section of the lake during winter.

Owing to the draught of the research vessels, the standard survey programme was restricted to the area deeper than 0.6 m. However, as *P. microps* appeared to be abundant in the

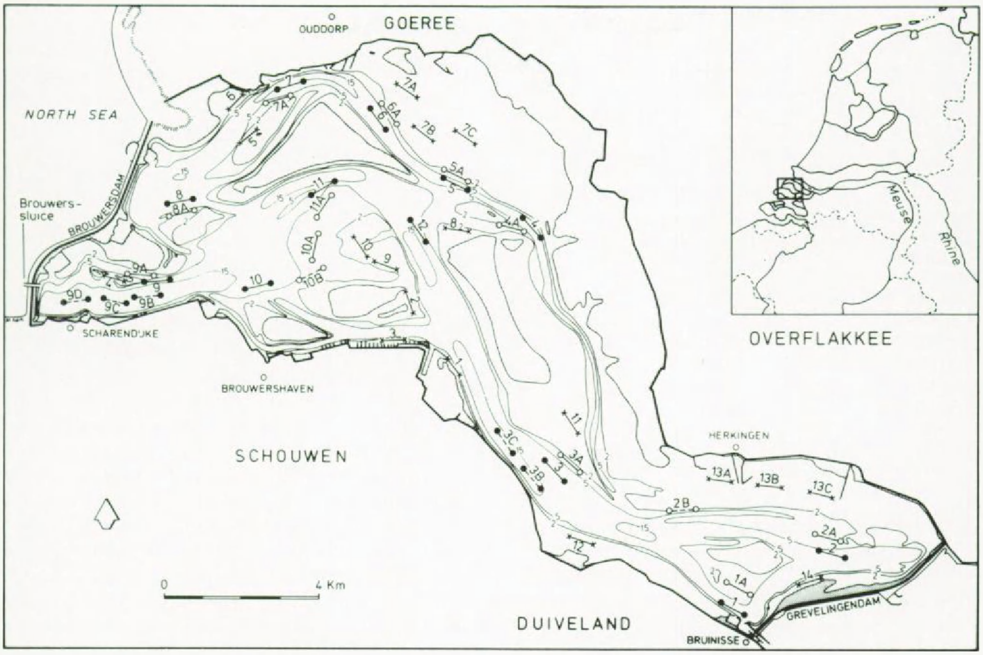


Fig. 1. Map of Lake Grevelingen (SW Netherlands), showing the positions of the fixed sampling stations in the strata 0 to 2 m (x——x), 2 to 5 m (o——o) and >5 m (●——●). Incidentally fished stations are indicated by interrupted lines. Depth contours are in metres, while the land areas and islands are hatched.

shallowest parts of the lake, additional information from the 0 to 0.6 m (18 km^2) zone was obtained biweekly on 16 selected locations from June 1981 onwards by towing the 1.9 m trawl by hand at a speed of approximately 0.7 m·s^{-1}, covering 285 m^2 per haul (ERENST & DE GRAAF, 1983).

All fish of each haul, or a subsample in case of large catches, were collected and frozen. In the laboratory, total length was measured in 5 mm classes. The biomass value was calculated on the basis of estimated length-weight relationships.

Catches were converted into absolute densities by considering gear efficiencies for *P. microps* and *P. minutus*, which were assessed in separate experiments (Table 1). Due to mesh selection, fishes smaller than 20 mm were not caught quantitatively and, hence, were disregarded. In case of the 1.9 m trawl, efficiencies found in the 56 to 60 mm length class were supposed to apply to larger individuals too (*cf.* Table 1). The efficiency values obtained for *P. microps* and *P. minutus* were assumed to apply to *Gobius niger* too. The total number of fish for the whole lake and the 95% confidence limits were estimated by means of standard methods for stratified (random) sampling (SAMPFORD, 1962; COCHRAN, 1963).

2.3. ANALYSIS OF FOOD COMPOSITION

Food composition was studied by analyzing the gut and stomach contents of *P. microps* and *P. minutus* caught in water deeper than 0.6 m during the period August through November 1980 only. The fishes were anaesthetized with MS 222 to prevent regurgitation and preserved in 4% formalin, which hardly affects the lengths of the specimens (DE GRAAF, 1979). In the laboratory, the fishes were divided into 5 mm size classes. The ingested macrofauna was identified to the highest possible taxon and counted, while complete prey organisms were measured. No attempt was made to identify small prey such as Copepoda, Foraminifera and Ostracoda to the species level. In the case of fragmented animals,

TABLE 1

Gear efficiencies by size class of the 1.9 m and 3 m beam trawl, respectively equipped with 0 (E_0) and 1 tickler chain (E_1), for *Pomatoschistus microps* and *P. minutus*. (After DOORNBOS *et al.*, 1986). Between brackets the selectivity of the 1.9 m trawl when towed by hand (*cf.* ERENST & DE GRAAF, 1983).

	1.9 m Beam trawl		3 m Beam trawl	
Length (mm)	E_0 (%)	E_1 (%)	E_0 (%)	E_1(%)
21-25	19.2	26.4 (24.9)	12.5	15.7
26-30	24.0	36.1 (28.3)	22.7	36.8
31-35	24.1	36.5 (26.7)	28.5	54.8
36-40	22.2	32.2 (21.8)	32.8	73.0
41-45	19.9	27.7 (15.2)	34.2	80.5
46-50	17.3	22.8 (8.8)	34.7	83.3
51-55	14.1	17.6 (4.2)	35.0	84.8
56-60	10.4	12.1 (3.2)	35.0	85.0
61-65			35.0	85.0
66-70			35.0	85.0

TABLE 2

Length-weight relationships of the main epibenthic crustaceans eaten by the larger gobiid fish. Length (L) in mm and ash-free dry weight (W) in mg. After unpublished data of A. Fortuin (personal communication).

Species	*Relationship*
Praunus flexuosus	$W = 1.43 \times 10^{-3} L^{2.932}$
Gammarus locusta	$W = 5.23 \times 10^{-3} L^{2.567}$
Idotea chelipes	$W = 7.73 \times 10^{-3} L^{2.383}$

counts were based on numbers of some characteristic body segments.

Subsequently, the numbers of specimens of the most important prey species were converted into a corresponding ash-free dry weight (ADW). For that purpose, length-weight relationships were established for the main epibenthic crustaceans (Table 2). From unpublished data of C. BAKKER, a mean dry weight (DW) of 0.01 mg for copepods was derived, which was multiplied by 0.7 to obtain the corresponding ADW figure. Foraminifera weighed on average also 0.01 mg DW (*cf.* GLAZENBURG, 1982).

2.4. ESTIMATION OF FOOD CONSUMPTION

Food consumed by fish is used for metabolism, maintenance of the body and for growth, while undigestible parts are excreted (ELLIOTT, 1976; BRETT & GROVES, 1979).

When fish are kept at different food rations and food intake is plotted against growth, a more or less linear relationship follows:

$$\text{Growth} = -a + b \times \text{Food intake}$$

or

$$\text{Food intake} = m + c \times \text{Growth}$$

where a gives the weight loss of fasting fish and m the maintenance food requirements to avoid weight loss. The maintenance food intake is related to metabolism (and therefore to the metabolic weight of the fish) and to water temperature. The net food conversion factor b (growth/food, <1) or c (food/growth, >1) gives the conversion of food into growth when excretion and metabolism have been taken into consideration. The net food conversion factor, maintenance requirements and temperature effects can be measured in laboratory experiments (BRAFIELD, 1985; SOOFIANI & HAWKINS, 1985). When these are known, the food intake of a fish population can be estimated on the basis of biomass, size distribution, growth (production) and water temperature.

FONDS *et al.* (1985) estimated the oxygen consumption, daily food intake and growth of juvenile plaice *Pleuronectes platessa* fed with chopped mussel meat. They calculated a net food conversion factor in ash-free dry weight of approximately 2.1 (*i.e.* food/growth) at higher water temperatures (14 to 22°C) and a daily maintenance food intake (maint. DFC in mg ADW per day per fish) of approximately:

$$\text{maint. DFC} = 1.5\ W^{0.78} \times e^{0.06\ T}$$

where W is the fresh weight (FW) of the fish in g and T the water temperature in°C.

For young cod *Gadus morhua* fed with mussel meat the net food conversion factor similarly ranged from 1.8 (at 15°C) to 2.1 (at 5°C). However, for young cod fed with chopped shrimps, the conversion factor appeared to be lower: 1.4 (15°C) to 1.6 (5°C). The conversion of food proteins into proteins of growth of the fish was similar for the groups fed with mussel meat or shrimps, which suggests that the glycogen in the mussel meat (approximately 20%) was hardly utilized by the fish. The standard oxygen consumption of both the young cod and the young plaice, in mg oxygen per fish per day, appeared to be approximately equal to the calculated maintenance food intake in mg ADW per fish per day. Hence, the oxygen consumption of non-fed resting fish can be used for the calculation of the maintenance food intake, when the actual maintenance food requirements are not known (M. FONDS, personal communication).

Since the gobies in Lake Grevelingen mainly feed on crustaceans, an average value of 1.5 times growth has been used in the calculation of the food intake from the growth rate of the fish. For the calculation of the maintenance food requirements, the measurements of the oxygen consumption of *Pomatoschistus microps* and *P. minutus* by FONDS & VELDHUIS (1973) were used, giving the oxygen consumption of the gobies at rest (R) in μ grat O per fish per hour, in relation to the fresh weight of the fish in gram (W):

$$\log R = \log k + b \log W$$

or

$$R = k\ W^b$$

The exponent b appeared to be 0.81 ± 0.02 in *P. microps* and 0.85 ± 0.04 in *P. minutus*. Since the difference is small, the respiration at rest was recalculated for a common "metabolic weight exponent" of 0.8 (WINBERG, 1956) on the basis of the length-weight relationship of both species in Lake Grevelingen (Table 3). Subsequently, these values were plotted semi-logarithmically against temperature (Fig. 2) and the next regressions

TABLE 3

Parameters of oxygen consumption at rest (R) in *Pomatoschistus microps* and *P. minutus* in relation to body weight (W in g fresh weight) at various water temperatures in °C, according to FONDS & VELDHUIS (1973). On the basis of the length-weight relationship for the two species in Lake Grevelingen, the coefficient k_1 and the exponent b of the original regression $R_1 = k_1 W^b$ were recalculated to a common weight exponent of b = 0.8, giving $R_2 = k_2 W^{0.8}$. R_1 expressed in μ grat O per hour; R_2 in mg O_2 per day (mg oxygen per day = μ grat O per hour x 24 x 16/1000).

Temp.	*P. microps*			*P. minutus*		
°C	k_1	*b*	k_2	k_1	*b*	k_2
5	0.687	0.816	1.835	0.596	0.878	1.368
10	0.746	0.783	2.181	0.836	0.882	2.365
15	0.927	0.789	3.286	0.890	0.812	2.933
20	1.314	0.844	7.542	1.093	0.804	4.731
25	1.402	0.810	9.583	1.342	0.880	7.602

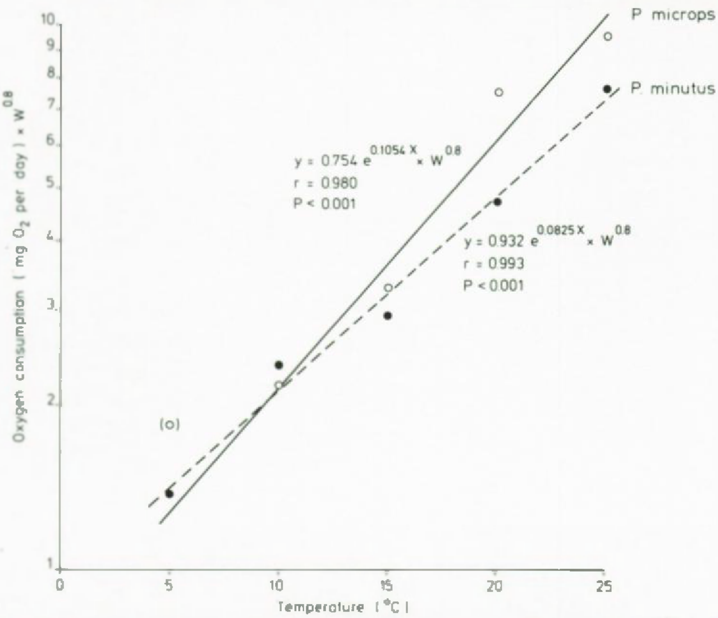


Fig. 2. Oxygen consumption at rest of *Pomatoschistus microps* and *P. minutus* in relation to water temperatures on the basis of k_2 values shown in Table 3. In constructing the regression lines, the k_2 for *P. microps* at T = 5°C has been excluded since the high value seems unrealistic for a thermophile species, certainly in comparison with *P. minutus*. W is body weight in g FW.

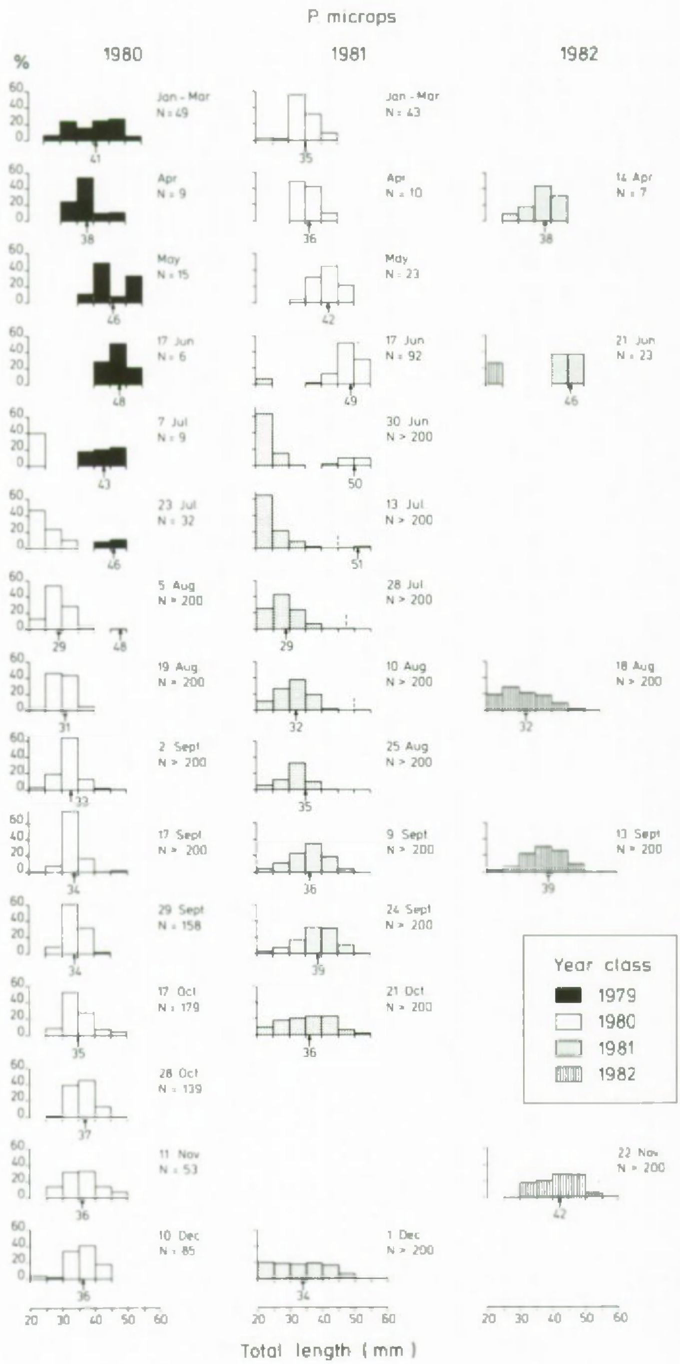

P. microps
%
1980
1981
1982
Jan - Mar N = 49
Jan - Mar N = 43
Apr N = 9
Apr N = 10
14 Apr N = 7
May N = 15
May N = 23
17 Jun N = 6
17 Jun N = 92
21 Jun N = 23
7 Jul N = 9
30 Jun N > 200
23 Jul N = 32
13 Jul N > 200
5 Aug N = 200
28 Jul N > 200
19 Aug N = 200
10 Aug N > 200
18 Aug N > 200
2 Sept N > 200
25 Aug N > 200
17 Sept N = 200
9 Sept N > 200
13 Sept N = 200
29 Sept N = 158
24 Sept N > 200
17 Oct N = 179
21 Oct N = 200
28 Oct N = 139
11 Nov N = 53
22 Nov N = 200
10 Dec N = 85
1 Dec N > 200
Year class
1979
1980
1981
1982
20 30 40 50 60
Total length (mm)

TABLE 4

Length-weight relationships for Gobiidae observed in 3 years. Length (L) in mm and fresh weight (W) in g.

Species	*1980*	*1981*	*1982*
P. microps	$W = 5.51 \times 10^{-6} L^{3.132}$	$W = 6.78 \times 10^{-6} L^{3.082}$	$W = 5.75 \times 10^{-6} L^{3.150}$
P. minutus	$W = 3.68 \times 10^{-6} L^{3.189}$	$W = 2.65 \times 10^{-6} L^{3.281}$	$W = 4.80 \times 10^{-6} L^{3.132}$
G. niger	$W = 6.47 \times 10^{-6} L^{3.145}$	$W = 4.42 \times 10^{-6} L^{3.241}$	$W = 4.33 \times 10^{-6} L^{3.242}$

computed:

P. microps $R = 0.75\ W^{0.8} \times e^{0.105\ T}$

P. minutus $R = 0.93\ W^{0.8} \times e^{0.083\ T}$

where W is weight in g FW and R is the oxygen consumption in mg per day, the latter probably being more or less equal to the maintenance food intake in mg ADW per day.

By assuming an ash-free dry weight proportion of about 17% (DE VLAS, 1979) the calculated food intake (in mg ADW) can be converted into gram fresh weight (FW) by dividing the coefficients 0.75 and 0.93 by 170.

Thus we obtain the following final equations to estimate the total daily food consumption of the main gobiid species in Lake Grevelingen:

P. microps $F = 1.5\ dW + 0.0044\ W^{0.8} \times e^{0.105\ T}$

P. minutus $F = 1.5\ dW + 0.0055\ W^{0.8} \times e^{0.083\ T}$

where F is the food intake in gram FW per day, dW is the change in weight (*i.e.* growth or production) in g FW per day, W is the fresh weight of the fish in g and T is the water temperature in °C.

Annual food consumption can be estimated by summing the daily food intakes over the season. For *P. minutus* the water temperatures over the season were derived from the water column in the central part of the lake, while for *P. microps* temperatures in the littoral zone (only during summer 1981) were used.

To estimate the annual food consumption of the populations of the two species in Lake Grevelingen, their numbers as well as their growth in length and weight have been calculated back to the moment of hatching, on the basis of the catch data (of individuals >20 mm) from August onwards, since most of the production (and hence consumption) in young gobiid fish takes place in the period May to August. According to FONDS (1970, 1973) and RUSSELL (1976) the newly hatched larvae of *P. microps* and *P. minutus* are approximately 2.5 mm and 3.0 mm long, respectively.

Because FONDS (1971, 1973) observed 2 different species of closely resembling sand gobies in the Wadden Sea, *viz. Pomatoschistus minutus* Pallas and *Pomatoschistus lozanoi* de Buen, a sample from Lake Grevelingen was analyzed on morphological characteristics and all the animals proved to belong to *P. minutus* (M. FONDS, personal communication).

3. RESULTS

3.1. LENGTH-WEIGHT RELATIONSHIP

Only minor differences were found between the depth zones and seasons distinguished, and therefore all data over one calendar year were combined to estimate the length-weight relationship for each gobiid species separately. Even between different years, the variation appeared to be relatively small (Table 4).

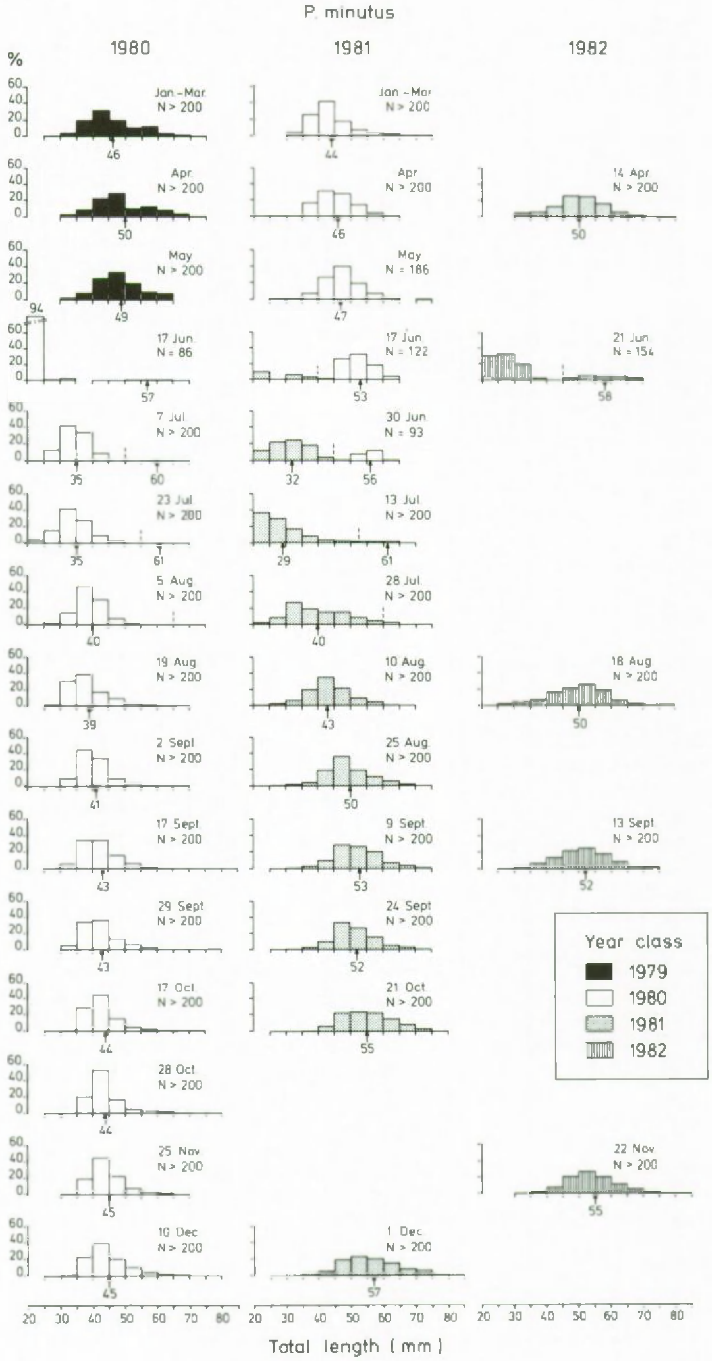
3.2. LENGTH-AGE DISTRIBUTION

Pomatoschistus microps

During the first 6 months of 1980 and 1981, as well as in April 1982, only one age group could be distinguished in the size-frequency histograms of *P. microps* (Fig. 3). In that period the length of the adult animals ranged from 20 to 55 mm.

In 1981 as well as in 1982, young of the year of over 20 mm were first caught in the second half of June, while in 1980 that was only the case on 7 July. From mid-July onwards, the catches were dominated completely by the new O-group fish (Fig. 3).

← Fig. 3. Size-frequency histograms of *Pomatoschistus microps* in 1980, 1981 and 1982. The year classes distinguished as well as the average lengths of the O- and I-group fish (arrows) are indicated.


P. minutus
1980
1981
1982
%
Year class
1979
1980
1981
1982
Total length (mm)

← Fig. 4. Size-frequency histograms of *Pomatoschistus minutus* in 1980, 1981 and 1982. The year classes distinguished as well as the average lengths of the O- and I-group fish (arrows) are indicated.

Pomatoschistus minutus

Over the 3 successive years, 2 distinct age classes could be recognized in the size-frequency histograms of *P. minutus* only from mid-June till July (Fig. 4). During the first 6 months, the I-group fish measured 20 to 80 mm.

The new recruits entered the catches in the second half of June, while from the start of July onwards the new O-group fish dominated the size-frequency distributions (Fig. 4).

Gobius niger

During 1980 through 1982, 5 year classes could be distinguished in the size-frequency histograms of *G. niger*, of which a maximum of 3 were present at the same time (Fig. 5). Throughout 1980, the size-frequency histograms were dominated by the 1979 year class, while the few large individuals probably belonged to the 1978 year class.

Recruits from the 1980 year class were first

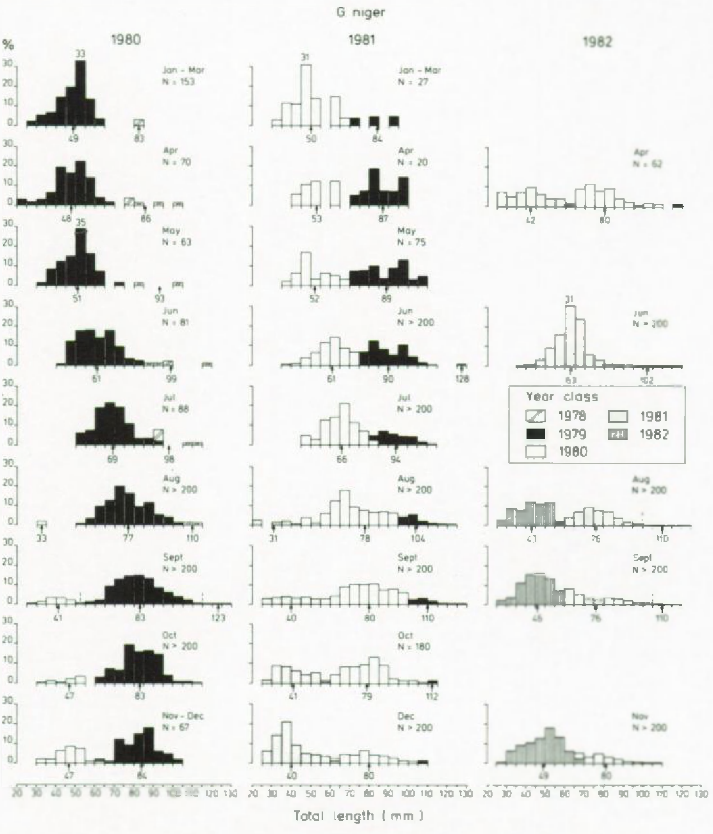


Fig. 5. Size-frequency histograms of *Gobius niger* during 1980 to 1982. The year classes distinguished (by eye) as well as the average lengths of the O-, I- and II-group fish (arrows) are indicated.

TABLE 5

Values observed for mean density (N per 1000 m^2) and biomass (B in g fresh weight per 1000 m^2) of *Pomatoschistus microps* (total length >20 mm) in the depth zones distinguished during 1980 to 1982. A - means: not sampled.

	0 to 0.6 m		*0.6 to 2 m*		*2 to 5 m*		*5 to 20 m*		*>20 m*	
Date	*N*	*B*	*N*	*B*	*N*	*B*	*N*	*B*	*N*	*B*
1980										
15 January	-	-	0	0	1	0	1	1	-	-
29 January	-	-	0	0	1	1	1	0	-	-
18 February	-	-	1	0	0	0	2	1	-	-
10 March	-	-	1	1	1	0	1	0	-	-
25 March	-	-	2	2	0	0	0	0	-	-
11 April	-	-	3	2	0	0	0	0	-	-
17 April	-	-	0	0	2	1	0	0	-	-
7 May	-	-	3	2	0	0	0	0	-	-
20 May	-	-	6	6	0	0	0	1	-	-
3 June	-	-	5	3	0	0	0	0	-	-
17 June	-	-	4	4	0	0	0	0	-	-
7 July	-	-	3	1	0	0	0	0	-	-
23 July	-	-	12	4	0	0	1	0	-	-
5 August	-	-	155	35	1	1	1	0	-	-
19 August	-	-	135	35	2	1	0	0	-	-
2 September	-	-	106	34	5	1	0	0	-	-
17 September	-	-	138	49	0	0	0	0	-	-
29 September	-	-	74	27	3	1	0	0	-	-
17 October	-	-	81	33	0	0	1	0	-	-
28 October	-	-	69	31	0	0	1	0	-	-
11 November	-	-	5	2	7	3	14	7	3	3
25 November	-	-	7	3	2	1	6	3	0	0
10 December	-	-	1	0	4	2	22	8	108	65
1981										
9 January	-	-	2	1	1	0	1	0	0	0
5 February	-	-	1	0	1	0	3	1	14	5
10 March	-	-	4	1	0	0	1	0	0	0
25 March	-	-	3	1	0	0	3	1	0	0
7 April	-	-	5	2	0	0	0	0	0	0
22 April	-	-	0	0	0	0	0	0	0	0
4 May	-	-	2	1	0	0	0	0	0	0
20 May	-	-	5	4	0	0	0	0	0	0
2 June	-	-	3	2	1	1	0	0	0	0
17 June	177	229	4	4	1	1	2	2	0	0
30 June	616	212	6	4	1	1	1	1	0	0
13 July	3075	545	21	6	7	2	3	2	0	0
28 July	5905	1327	83	23	25	5	5	1	19	5
10 August	8185	2519	223	67	326	87	15	5	9	2
25 August	13897	5640	396	153	43	18	15	6	0	0
9 September	15152	7288	222	88	81	39	46	25	0	0
24 September	12075	7589	465	216	91	37	43	20	3	1
21 October	3981	1933	269	158	56	21	78	38	38	24
1 December	867	343	0	0	98	36	118	64	103	76
1982										
14 April	4	2	0	0	0	0	0	0	0	0
21 June	31	19	2	2	0	0	0	0	0	0
18 August	4434	1330	86	30	2	1	0	0	0	0
13 September	4051	2319	129	77	19	10	0	0	0	0
22 November	-	-	0	0	11	8	24	19	5	5

caught in August. This year class appeared to be less strong than that of 1979, since in November/December the catches were still dominated by I-group fish. Both year classes could be recognized in the length-frequency distributions till April 1982. From August 1981 onwards, the 1981 year class was easily identifiable, as was the 1982 year class one year later (Fig. 5).

3.3. DENSITY AND BIOMASS

Pomatoschistus microps

By far the highest numbers of *P. microps* (>20 mm) were found in the littoral zone of the lake (Table 5). In September 1981, the density in the 0 to 0.6 m stratum amounted even to 15 common gobies per m^2, with a biomass of over 7 g $FW \cdot m^{-2}$. During the summer of 1982, the density was less high, *viz.* 4 fishes per m^2. In 1980, however, the most important 0 to 0.6 m zone was not sampled. Over August to September (in 1981 as well as in 1982), the density in the 0 to 0.6 m stratum was on average 41.5 times higher than in the 0.6 to 2 m zone (*cf.* Table 5). From this an estimate of the *P. microps* density in the littoral zone for August 1980 can be derived, *viz.* about 6 fishes per m^2.

For the entire Lake Grevelingen, year class 1981 as O-group was assessed at 282 million *P. microps* (*i.e.* on average 2.6 fishes per m^2) in early September, of which ⅔ had already disappeared one month later. The fast decrease in numbers continued during the winter, through 0.6 million in April, to as few as 10 000 individuals surviving as I-group in September 1982 (Fig. 6). In August 1982, the total number of O-group *P. microps* amounted to only 82 million individuals, while for August 1980 this total was approximately 110 million fish.

In 1981 the highest biomass, *i.e.* 133 tons FW (or 1.2 $g \cdot m^{-2}$) was estimated in September. In 1982, a maximum biomass of only 44 tons was assessed (*cf.* Table 5).

Pomatoschistus minutus

Contrary to the common goby, the sand goby was more evenly spread over the lake. Only from October to February were concentrations found locally in deep pits with a silty sediment (Table 6). Densities were much higher in 1980 than in 1981 and 1982.

In early August 1980 the total number of O-group *P. minutus* was assessed at 424 million (*i.e.* 3.9 fishes per m^2) with a biomass of 203 tons FW. Afterwards the numbers of this year class declined constantly to approximately 150 000 individuals in early August 1981 (Fig. 6). In 1981 and 1982, the peak numbers of the O-group amounted only to 29 and 15 million sand gobies, respectively (Fig. 6; Table 6).

Gobius niger

The black goby was most abundant in the deeper parts of the lake (Table 7). The peak numbers for all year classes combined in the consecutive years were assessed at 3.7, 1.3 and 5.1 million individuals. The biomass figures amounted roughly to 24, 7 and 13 tons FW.

3.4. MORTALITY AND MAXIMUM AGE

From the computed regression lines through the assessed numbers of gobies for the whole lake, it can be seen that in both gobiid species (>20 mm) the mortality rate was fairly constant over the year (Fig. 6). In *P. minutus*

$$z = (\Delta t)^{-1} \cdot \ln n_1 n_2^{-1}$$

varied from 0.0186 d^{-1} in year class 1981 to 0.0219 d^{-1} in year class 1980, which corresponds with an average monthly mortality of approximately 46%. Hence, on average only 0.1% of the O-group animals present in August survives until the next summer. In late March/early April, as few as 1 to 2% of the original year class size are involved in reproduction.

The mortality rate in *P. microps*, year class 1981, was even somewhat higher, *viz.* $z = 0.0275$ d^{-1} (or 57% per month). From mid-June (when the 0 to 0.6 m zone was sampled for the first time) to August 1981, the mortality rate in I-group *P. microps* was 0.0261 d^{-1} (~55% per month), which is similar to the value obtained for the 1981 year class. However, if the assessed numbers of *P. microps* in August 1980 (see Chapter 3.3.) are accepted, the estimate of the mortality rate in year class 1980 would have been much lower, *viz.* approximately 0.014 d^{-1}.

In Lake Grevelingen a maximum age of approximately 1½ years was inferred both for the sand goby and the common goby, while the black goby grew at least 3 years old (context also Figs 3, 4, 5 and 8).

TABLE 6

Values observed for mean density (N per 1000 m^2) and biomass (B in g fresh weight per 1000 m^2) of *Pomatoschistus minutus* (total length >20 mm) in the depth zones distinguished during 1980 to 1982. A · means: not sampled.

	0 to 2 m		*2 to 5 m*		*5 to 20 m*		*>20 m*	
Date	*N*	*B*	*N*	*B*	*N*	*B*	*N*	*B*
1980								
15 January	2	2	5	4	23	24	-	-
29 January	2	2	2	2	25	18	-	-
18 February	6	7	4	5	48	32	-	-
10 March	7	7	1	0	10	7	-	-
25 March	10	10	1	0	5	3	-	-
11 April	41	51	1	2	25	20	-	-
17 April	13	17	4	3	50	42	-	-
7 May	11	14	10	10	52	43	-	-
20 May	10	10	1	0	19	18	-	-
3 June	13	16	8	10	8	9	-	-
17 June	30	24	517	43	395	48	-	-
7 July	392	144	209	66	265	101	-	-
23 July	1121	485	2058	673	3485	982	-	-
5 August	1348	773	5221	2429	6457	3078	-	-
19 August	1173	847	3448	1195	4766	2139	-	-
2 September	841	607	3193	1642	3759	1791	-	-
17 September	752	615	1159	749	3243	1823	-	-
29 September	350	315	683	484	2282	1293	-	-
17 October	226	187	344	212	2681	1740	-	-
28 October	183	174	148	95	2840	1925	-	-
11 November	6	4	33	22	465	304	1909	1344
25 November	31	27	21	14	257	173	6824	4811
10 December	8	6	42	33	434	262	7200	5958
1981								
9 January	16	12	11	6	84	51	309	186
5 February	11	8	18	11	131	81	2653	2023
10 March	6	4	1	1	18	12	165	97
25 March	3	2	8	6	116	79	47	29
7 April	23	19	7	5	7	4	202	146
22 April	0	0	1	1	14	11	252	224
4 May	4	4	2	3	11	9	76	59
20 May	3	3	1	1	11	9	0	0
2 June	2	3	0	0	7	7	42	37
17 June	5	2	6	8	18	21	4	5
30 June	13	4	12	4	7	7	0	0
13 July	101	23	204	31	140	43	5	4
28 July	15	16	143	49	230	159	298	204
10 August	39	42	291	190	272	186	25	23
25 August	30	43	54	50	185	182	43	46
9 September	36	60	153	164	630	787	399	501
24 September	51	90	100	106	472	523	377	438
21 October	19	38	3	4	138	187	1359	2114
1 December	0	0	19	25	456	706	2756	4897
1982								
14 April	1	2	1	2	9	10	46	51
21 June	9	3	16	4	3	4	1	1
18 August	148	195	78	77	164	152	430	416
13 September	48	73	49	67	199	211	2	3
22 November	0	0	13	16	510	715	920	1366

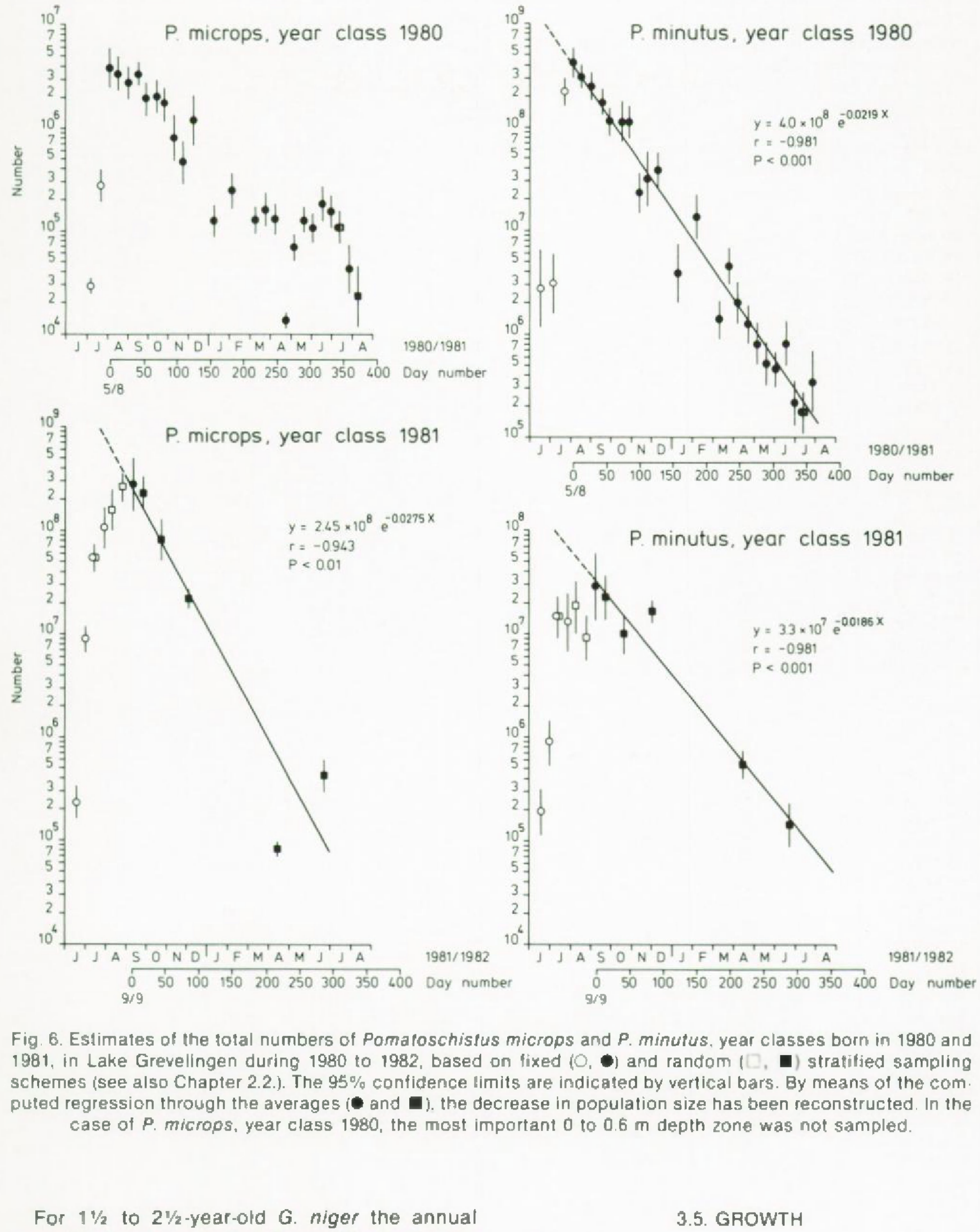


Fig. 6. Estimates of the total numbers of *Pomatoschistus microps* and *P. minutus*, year classes born in 1980 and 1981, in Lake Grevelingen during 1980 to 1982, based on fixed (○, ●) and random (□, ■) stratified sampling schemes (see also Chapter 2.2.). The 95% confidence limits are indicated by vertical bars. By means of the computed regression through the averages (● and ■), the decrease in population size has been reconstructed. In the case of *P. microps*, year class 1980, the most important 0 to 0.6 m depth zone was not sampled.

For 1½ to 2½-year-old *G. niger* the annual mortality (over the period August/September to August/September of the next year) varied from 97.3% in year class 1979 to 98% in year class 1980, resulting in an average mortality rate of 0.0103 d^{-1} (or 27% per month).

3.5. GROWTH

Pomatoschistus microps

From early spring to the beginning of August, the average length of the I-group *P. microps* increas-

TABLE 7

Values observed for mean density (N per 1000 m^2) and biomass (B in g fresh weight per 1000 m^2) of *Gobius niger* (total length >20 mm) in the depth zones distinguished during 1980 to 1982. A - means: not sampled.

	0 to 2 m		*2 to 5 m*		*5 to 20 m*		*>20 m*	
Date	*N*	*B*	*N*	*B*	*N*	*B*	*N*	*B*
1980								
15 January	0	0	3	4	3	6	-	-
29 January	0	0	3	8	3	5	-	-
18 February	0	0	3	4	5	7	-	-
10 March	0	0	1	1	4	5	-	-
25 March	0	0	4	5	5	8	-	-
11 April	0	0	3	5	13	24	-	-
17 April	0	0	9	15	10	24	-	-
7 May	0	0	8	15	14	24	-	-
20 May	3	4	2	3	4	14	-	-
3 June	3	5	10	28	7	37	-	-
17 June	5	14	15	44	6	21	-	-
7 July	1	4	14	49	10	47	-	-
23 July	2	9	7	49	11	58	-	-
5 August	1	3	31	141	50	306	-	-
19 August	3	9	38	191	72	521	-	-
2 September	0	0	31	103	81	628	-	-
17 September	0	0	11	55	75	492	-	-
29 September	0	0	15	71	80	604	-	-
17 October	0	0	2	7	44	325	-	-
28 October	0	0	2	5	30	202	-	-
11 November	0	0	0	1	2	2	14	112
25 November	0	0	3	12	4	25	80	586
10 December	0	0	0	0	5	31	6	30
1981								
9 January	0	0	0	0	1	1	0	0
5 February	0	0	5	11	1	1	0	0
10 March	0	0	1	3	1	6	4	1
25 March	0	0	0	0	3	7	0	0
7 April	0	0	1	4	1	12	0	0
22 April	0	0	1	1	2	7	23	198
4 May	0	0	3	12	2	15	16	153
20 May	0	1	2	8	3	18	11	157
2 June	5	27	5	15	6	43	1	21
17 June	3	18	20	88	16	131	1	10
30 June	3	33	5	21	8	53	1	21
13 July	1	3	4	27	8	49	0	0
28 July	1	4	4	18	4	27	0	0
10 August	1	4	7	32	12	77	2	20
25 August	1	1	2	14	8	61	0	3
9 September	0	0	3	13	16	131	26	330
24 September	2	16	6	20	28	151	29	283
21 October	0	0	1	2	3	11	19	135
1 December	0	0	2	2	10	26	16	94
1982								
14 April	0	0	0	0	1	1	6	46
21 June	10	33	13	48	8	26	0	1
18 August	4	6	9	21	27	94	29	166
13 September	18	43	40	81	93	265	0	7
22 November	0	0	9	11	29	49	277	1109

ed roughly from 41 to 48 mm in 1980 and from 35 to 51 mm in 1981, while the lengths in April and June 1982 were similar to those observed in the same months of the previous years (Fig. 3).

Around mid-August, the O-group fish had already attained an average size of 31 mm in 1980 and 32 mm in 1981 and 1982. In 1980, the maximum average size of the O-group, 37 mm, was reached at the end of October, while in 1981 this was already the case in September, when an average length of 39 mm was attained. During the summer months, the mean daily length increment of *P. microps* was 0.16 mm to 0.21 mm in 1980 and 1981, and even 0.27 mm in 1982.

Due to the disappearance of larger animals and the appearance of a (small) second breeding-wave in 1980 and particularly in 1981, the average size decreased towards the end of the year (Fig. 3). Although on the west coast of Sweden, in some years, also a second cohort could be distinguished in the recruitment of *P. microps* and *P. minutus*, its origin remains unknown (PIHL & ROSENBERG, 1982).

Based on the size-frequency histograms (Fig. 3), von Bertalanffy growth curves for length and weight have been estimated separately for O- and I-group fish. In these, data affected by mesh selection (*i.e.* O-group in June and July) as well as figures from the winter months have been excluded. In 1980 as well as in 1981, the mean maximum attainable length ($\overline{L}_\infty$) and weight ($\overline{W}_\infty$) in O-group *P. microps* were estimated at 39 mm and 0.6 g FW, respectively (Fig. 7). However, growth in 1981 was much faster than in 1980. In 1982 the O-group *P. microps* attained an average length of 42 mm. This means that growth in 1982 must

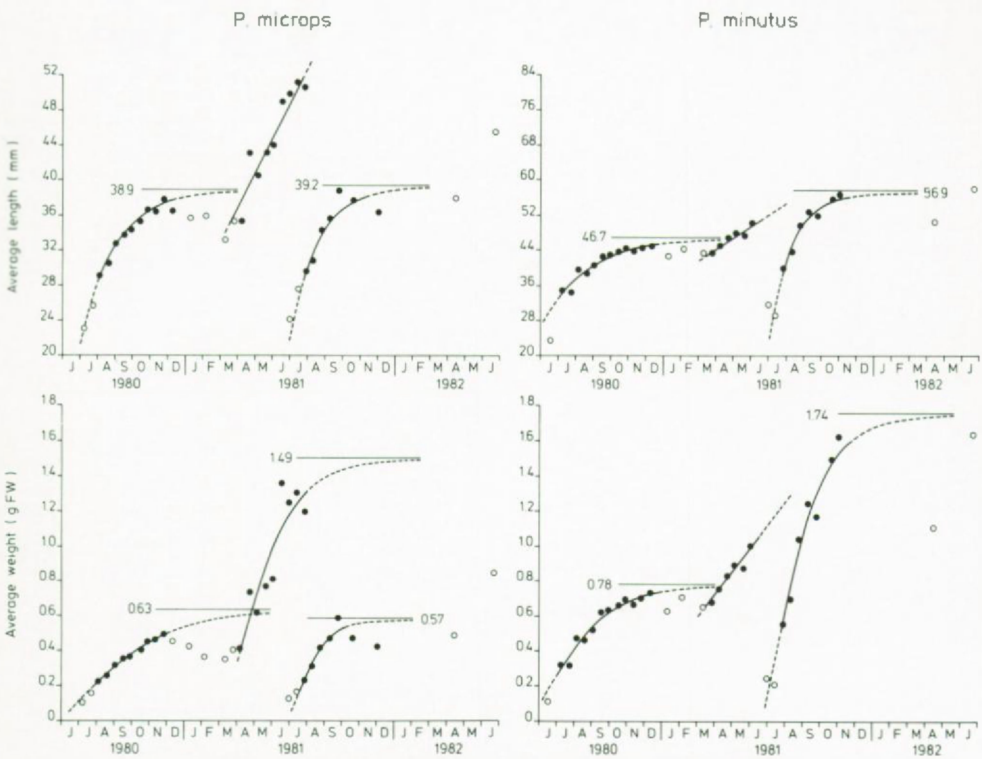


Fig. 7. Estimated von Bertalanffy growth curves for length and weight of O- and I-group *Pomatoschistus microps* and *P. minutus*. Actually observed values are indicated, of which only the full points were used to construct the curves (see text).

have been even faster than in 1981 (*cf.* Figs 3 and 7).

Length increment of the I-group *P. microps*, year class 1980, was practically linear from April through July (1981). The mean maximum attainable weight in the I-group fish was estimated at approximately 1.5 g FW (Fig. 7).

Pomatoschistus minutus

The average length of the adult fish of the 1979 year class increased from about 46 mm in the early spring of 1980 to 61 mm in July (Fig. 4). Already in the first half of July, the new recruits of the 1980 year class had reached an average

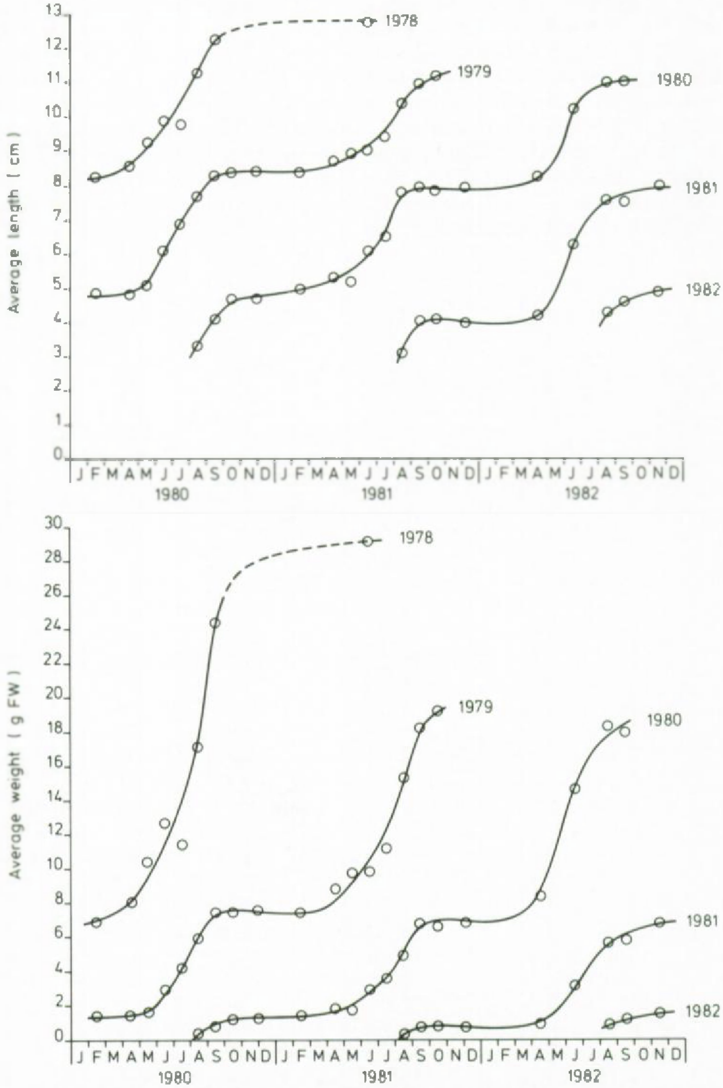


Fig. 8. Length and weight changes of the year classes distinguished (in Fig. 5) of *Gobius niger*. The curves were fitted by eye.

size of 35 mm. At the end of their first year, they measured on average 45 mm. The next summer, a mean maximum length of approximately 61 mm was attained, which is similar to that of the I-group in 1980.

Compared with 1980, the O-group of 1981 grew very fast, particularly from the end of July onwards, the average length having increased from 40 mm to 57 mm by early December (Fig. 4). However, the next year their growth was negligible, the average size being 58 mm at the end of June 1982. During the summer months, the length increment of the O-group *P. minutus* was on average as little as 0.12 mm per day in 1980, 0.45 $mm \cdot d^{-1}$ in 1981 and 0.41 $mm \cdot d^{-1}$ in 1982.

Based on the von Bertalanffy growth curves, the mean maximum attainable length and weight of O-group *P. minutus* for the 1980 growing season were estimated at 47 mm and 0.8 g FW, respectively (Fig. 7). For the 1981 season a marked $\bar{L}_\infty = 57$ mm and $\bar{W}_\infty = 1.7$ g were estimated for the O-group. The growth of the 1982 year class, as O-group attaining an average length of 55 mm by the end of the year, was very similar to that of the O-group in 1981 (Fig. 4).

Gobius niger

With an average size of approximately 3.5 cm (0.4 g FW), black goby juveniles entered the catches in August (Fig. 8). At the end of their first year, they had attained an average length of about 5 cm (1.4 g). However, the 1981 year class reached only 4 cm (0.8 g) in that period. From April/May on, growth continued, resulting in an average size of 8 to 8.5 cm (7 to 8 g) at the end of their second year of life. In their third and last year, they reached an average maximum size of 11 to 12.5 cm (18 to 25 g), the fishes of the 1978 year class being significantly bigger than the 1979 and 1980 year classes (Fig. 8). The largest *G. niger* caught measured 13 cm (29 g FW). During the period May to August, the length increment of the dominant I-group fish was on average 0.28 mm per day in all 3 years, and varied from 0.17 mm to 0.24 mm per day in the II-group of *G. niger*.

3.6. PRODUCTION

The daily production of the *P. microps* and *P. minutus* populations was estimated numerically according to the procedure mentioned in CHAPMAN (1978), using the following equation:

$$P = (\ln \bar{W}_{t+1} - \ln \bar{W}_t)\,\bar{B} \qquad (\ln \frac{\bar{W}_{t+1}}{\bar{W}_t} \geq 0)$$

in which P is the daily fish production, $\bar{W}_t$ and $\bar{W}_{t+1}$ are the mean weights of the fish on 2 successive days, and $\bar{B}$ is the average biomass according to

$$\bar{B} = \frac{B_t + B_{t+1}}{2}$$

Annual production was estimated by summing the daily production figures over the year. Since most of the production is supposed to be realized during the juvenile stage, the numbers as well as the average lengths and weights were calculated back on the basis of mortality rates earlier assessed (*cf.* Fig. 6) and von Bertalanffy growth curves (*cf.* Fig. 7). In this way, in *P. microps* an annual production of 516 tons FW (or 0.8 g $ADW \cdot m^{-2}$) was obtained for the abundant year class 1981 (Table 8). From the second half of May till the beginning of September, when the maximum numbers were caught, a production of 506 tons (98%) had already been realized. The production in the littoral zone may even have amounted to as much as 4.8 g $ADW \cdot m^{-2} a^{-1}$, since approximately 99% of the population of the common goby was present exclusively in shallow water during June and July.

In 1980, the numerous O-group of *P. minutus* produced as much as 674 tons FW (*i.e.* 1.1 g

TABLE 8

Estimated values for annual production, consumption and derived P/C ratio of the O-group populations of *Pomatoschistus minutus* and *P. microps* for the entire Lake Grevelingen in 1980 and 1981.

Species	*Year*	*Production*		*Consumption*		*P/C ratio*
		tons FW	*g* $ADW \cdot m^{-2}$	*tons FW*	*g* $ADW \cdot m^{-2}$	
P. minutus	1980	674	1.06	1238	1.95	0.54
P. minutus	1981	90	0.14	185	0.29	0.49
P. microps	1981	516	0.81	994	1.56	0.52

ADW·m^{-2}·a^{-1}), of which 92% was already realized before the second week of August (Table 8). In contrast, the production in 1981 was only 90 tons FW (or 0.14 g ADW·m^{-2}·a^{-1}). Combining the 1981 figures of *P. microps* and *P. minutus* results in a total production of 5.6 g FW (1.0 g ADW)·m^{-2}·a^{-1}.

Production in 1982 will have been lower than in 1980 and 1981, since the populations of both species were less abundant.

3.7. DIET AND ANNUAL FOOD CONSUMPTION

Usually, only 4 to 5 food items made up more than 95% (by weight) of the gut and stomach contents of *P. microps* and *P. minutus* (A.K. GLAZENBURG, personal communication). The weight shares of these main species in the diets of the various size classes of the gobiids are given in Fig. 9. For *P. microps* of up to about 40 mm, the food consisted almost entirely of calanoid and harpacticoid copepods. Around that size, the fish switched to larger epibenthic crustaceans, such as the isopod *Idotea chelipes*, the amphipod *Gammarus locusta* and the mysid *Praunus flexuosus*.

In the prey choice of *P. minutus*, an identical shift was observed. However, the change from copepods to larger crustaceans proved to be more gradual (Fig. 9). The weight proportion of copepods in the diet decreased from ~95% in animals of 30 mm to less than 1% in animals of 65 mm. On the contrary, the share of *Idotea chelipes* increased from zero to 80%. The stomachs of the 40 to 60 mm size classes contained *Praunus flexuosus* and *Gammarus locusta* in almost equal proportions, *i.e.* varying roughly between 15 and 35% of the totals. In all size classes of *P. minutus*, foraminiferans contributed 3 to 7% to the total food intake.

In the stomachs of *P. minutus*, remains of other prey were also found, such as nematodes, polychaetes (*e.g. chaetae*) as *Nereis* sp., *Nephtys* sp., and *Flabelligera affinis*, juvenile molluscs as *Cerastoderma edule*, *Mytilus edulis* and *Macoma balthica*, ostracods, *Balanus* sp., *Neomysis integer*, *Schistomysis kervillei*, *Corophium volutator*, *Crangon crangon*, chironomids (larvae) and gobiid eggs, all in small quantities. In *P. microps*, also remains of ostracods and *Corophium volutator* were traced (GLAZENBURG, 1982).

For the 1980 year class of *P. minutus*, an annual consumption of 1238 tons FW (*i.e.* 1.95 g ADW·m^{-2}) was assessed, of which 87% was realized from April through July (Table 8). Consumption in the less abundant 1981 year class was only 185 tons FW (0.29 g ADW·m^{-2}·a^{-1}). Since for the 1981 year class of *P. microps* a consumption of 994 tons FW was estimated, the total food intake of both gobiid populations combined amounted to 1.9 g ADW·m^{-2}·a^{-1} (Table 8).

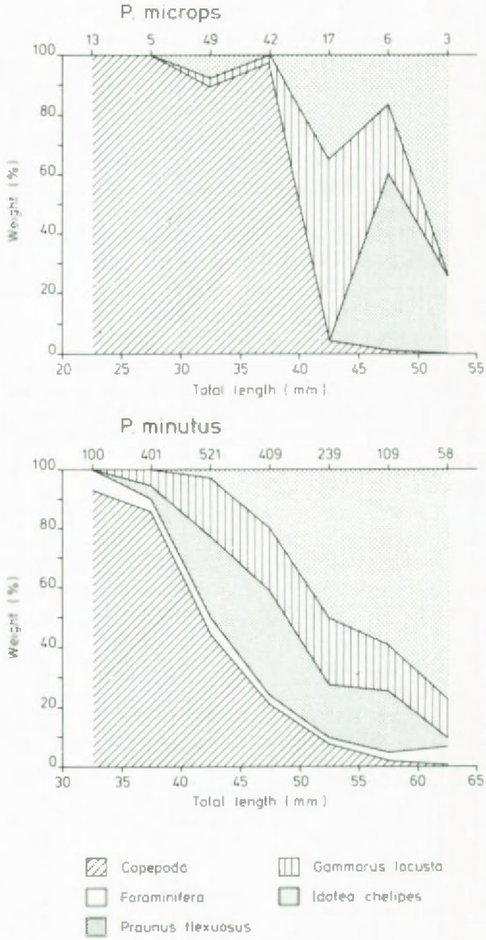


Fig. 9. Food composition in ash-free dry weight percentages in relation to size classes of *Pomatoschistus microps* and *P. minutus* during August through November 1980. Only the five main food items were considered (see text). The number of stomachs per size class investigated is indicated at the top of each graph. After data of GLAZENBURG (1982).

TABLE 9

Estimated values for consumption of each of the 5 main food items by the populations of *Pomatoschistus minutus* in 1980 and 1981, and *P. microps* in 1981.

	P. minutus (1980)		*P. minutus (1981)*		*P. microps (1981)*	
	tons ADW	*mg ADW* m^{-2}	*tons ADW*	*mg ADW* m^{-2}	*tons ADW*	*mg ADW* m^{-2}
Copepoda	191.9	1777	17.1	158	160.5	1486
Foraminifera	4.6	42	1.1	10	-	-
Praunus flexuosus	6.5	61	4.2	39	0.7	7
Gammarus locusta	5.3	49	3.4	32	4.0	37
Idotea chelipes	2.2	20	5.6	52	3.7	34
Total	210.5	1949	31.4	291	168.9	1564

Of course, production and consumption are strongly linked; due to high numbers and fast growth rates, both were highest during early summer.

The contribution of the different prey species to the annual amounts of food consumed by both gobiid populations was estimated on the basis of the size-frequency histograms at the sampling dates (*cf.* Figs 3 and 4), the diet composition of each size class (*cf.* Fig. 9) and the calculated food demands per period. As might be expected, predation was heaviest on copepods, *viz.* 1.8 g and 1.5 g $ADW \cdot m^{-2} a^{-1}$ in the 1980 and 1981 year classes of *P. minutus* and *P. microps*, respectively, and they supplied as much as 91% to 95% of the total food demands (Table 9). The annual predation on larger epibenthic crustaceans, such as *Praunus*, *Gammarus* and *Idotea*, was of minor importance, since they are only eaten by the largest fish, which are less numerous and grow relatively more slowly than juveniles. As the individuals of the 1981 year class of *P. minutus* were significantly bigger than those of the 1980 year class, the share of the larger crustaceans in the total consumption amounted to 42% in 1981 (Table 9).

4. DISCUSSION

4.1. POPULATION PARAMETERS DURING THE 1980 TO 1982 PERIOD

It turned out that the change from a fixed towards a random (stratified) sampling scheme did not significantly improve the accuracy of the data obtained: the standard errors of the means, and consequently the confidence limits obtained from both sampling schemes were of the same order of magnitude (*cf.* Fig. 6; DOORNBOS *et al.*, 1986). On the other hand, the choice of the strata proved to be of more importance, because *P. microps* was largely restricted to the littoral zone and *P. minutus* aggregated in deeper parts during winter. The doubling of the samples improved the data only slightly, since even in the larger strata the values for means and confidence limits hardly changed any more after 15 to 20 hauls had been taken (DOORNBOS *et al.*, 1986). In comparing fixed versus random sampling of fishes in the 105 km^2 large West Point Reservoir, U.S.A., KING *et al.* (1981) also found relatively few statistically significant differences in either means or variances between the two types of sampling schemes.

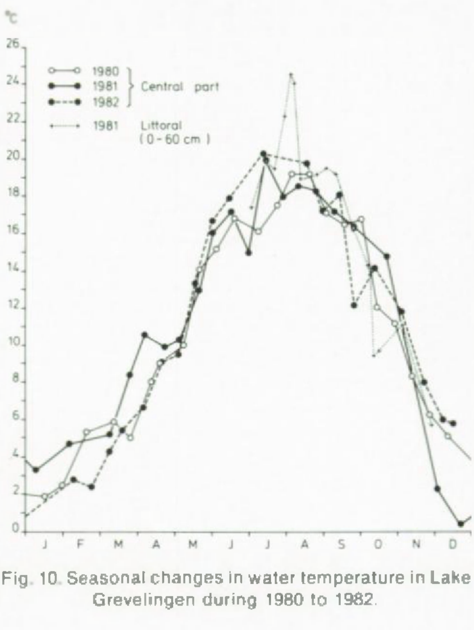


Fig. 10. Seasonal changes in water temperature in Lake Grevelingen during 1980 to 1982.

TABLE 10

Comparison of seasonal peak densities, annual production and consumption of *Pomatoschistus minutus*, *P. microps* and *Gobius niger* in different areas in NW Europe. In brackets the month the highest density was measured.

Area	*Water depth (m)*	*Year*	*Density ($N.m^{-2}$)*		*Prod. (g ADW $m^{-2}a^{-1}$)*	*Cons. (g ADW $m^{-2}a^{-1}$)*	*Reference*
P. minutus							
Western Wadden Sea	2-30	1961	0.2 [1]	(Oct.)			FONDS, 1973
	2-30	1962	0.25 [1]	(Nov.)			FONDS, 1973
	2-30	1963	0.2 [1]	(Nov.)			FONDS, 1973
	2-30	1964	0.4 [1]	(Oct.)			FONDS, 1973
North Sea coastal area	2-30	1963	0.3 [1]	(Oct.)			FONDS, 1973
	2-30	1964	0.5 [1]	(Oct.)			FONDS, 1973
Ythan estuary, E Scotland	shallow	1967	0.6 [2]	(Sept.)		0.3 [3]	HEALEY, 1971
	shallow	1968	0.5 [2]	(Sept.)		0.2 [3]	HEALEY, 1971
Balgzand, Dutch Wadden Sea	1-1.5[4]	1975	0.2	(July/Aug.)	0.03[5]	0.5 [5]	VAN BEEK, 1976
	1-1.5[4]	1976	0.4	(Oct.)			VAN DER GAAG, 1977
Askö area, E Sweden	0-0.5	1975	12.7	(Nov.)			ANEER & NELLBRING, 1977
	0-0.5	1976	~8	(Aug.)			ANEER & NELLBRING, 1977
Kvarnbukten, W Sweden	0-1	1976	2.0	(Sept.)	0.08[3]	0.31[3]	EVANS & TALLMARK, 1979; EVANS, 1984
	0-1	1977	1.3	(Sept.)	0.14[3]	0.32[3]	EVANS & TALLMARK, 1979; EVANS, 1984
	0-1	1978	3.9	(Aug.)	0.13		EVANS & TALLMARK, 1984
	0-1	1979	1.7	(July)	0.03		EVANS & TALLMARK, 1984
	0-1	1980	4.0	(July)	0.08		EVANS & TALLMARK, 1984
	2.5-10	1979	1.3	(Oct.)			EVANS & TALLMARK, 1984
	2.5-10	1980	0.5	(Sept.)			EVANS & TALLMARK, 1984
Gullmarsvik, W Sweden	0-0.7	1978	2.6	(July/Aug.)	0.24		PIHL & ROSENBERG, 1982
	0-0.7	1979	~0.6		0.09		PIHL & ROSENBERG, 1982
	0-0.7	1980			0.19		PIHL & ROSENBERG, 1982
Lake Grevelingen, SW Netherlands	0.7-1.5	1977	0.3	(Sept.)	0.03[5]		DE GRAAF, 1979
	0-50	1980	3.9	(Aug.)	1.1	1.95	This study
	0-50	1981	0.3	(Sept.)	0.14	0.29	This study
	0-50	1982	0.14	(Aug.)			This study
P. microps							
Nivå Bay, E Denmark	0-0.6	1963	~9	(Aug.)			MUUS, 1967

Ythan estuary, E Scotland	shallow	1967	0.1	(Oct.)			HEALEY, 1972a
	shallow	1968	0.1	(Nov.)			HEALEY, 1972a
Balgzand, Dutch Wadden Sea	1-1.5[4]	1975	1.6	(July)	0.04[5]	0.7 [5]	VAN BEEK, 1976
	1-1.5[4]	1976	1.6	(Sept.)	0.08	0.7	VAN DER GAAG, 1977
Gullmarsvik, W Sweden	0-0.7	1977	15.1	(Aug.)	0.6		PIHL & ROSENBERG, 1982
	0-0.7	1978	10.7	(July/Aug.)	0.4		PIHL & ROSENBERG, 1982
	0-0.7	1979	0.6		0.01		PIHL & ROSENBERG, 1982
	0-0.7	1980	0.8		0.04		PIHL & ROSENBERG, 1982
Sandvik, W Sweden	0-0.7	1977	12.0	(Sept.)	0.3		PIHL & ROSENBERG, 1982
	0-0.7	1978	25.0	(July/Aug.)	0.4		PIHL & ROSENBERG, 1982
Kvarnbukten, W Sweden	0-1	1978	8.5	(Aug.)	0.08[3]		EVANS & TALLMARK, 1984
	0-1	1980	1.9	(Oct.)	0.03[3]		EVANS & TALLMARK, 1984
Lake Grevelingen, SW Netherlands	0.7-1.5	1977	4.5	(Aug.)	0.19[5]		DE GRAAF, 1979
	0-0.6	1981	15.2	(Sept.)	4.8	9.3	This study
	0-0.6	1982	4.4	(Aug.)			This study
G. niger							
Lake Veere, SW Netherlands	2-20	1971	0.003[1]	(Sept.)			VAAS *et al.*, 1975
	2-20	1972	0.003[1]	(Nov.)			VAAS *et al.*, 1975
	2-20	1973	0.007[1]	(Nov.)			VAAS *et al.*, 1975
Oslofjord, S Norway	0-9	1981	0.02 [1]	(July/Aug.)			NASH, 1984
	0-9	1982	0.03 [1]	(June)			NASH, 1984
Stanswood Bay, S England	~ 1-4	1984	0.03	(Nov.)			VESEY & LANGFORD, 1985
Lake Grevelingen, SW Netherlands	0-50	1980	0.03	(Sept.)			This study
	0-50	1981	0.01	(Sept.)			This study
	0-50	1982	0.05	(Sept.)			This study

1) Not corrected for gear effiency.
2) Sampled at low tide when water was restricted to a narrow channel. Since the intertidal area was about twice the low tide channel, figures have to be halved to obtain actual densities.
3) Original figures in dry weight. They have been converted into g ash-free dry weight by assuming that 1 g DW is equivalent to approximately 0.85 g ADW (MCLUSKY, 1981).
4) At high tide.
5) Over July to November. Original figures in fresh weight. They have been converted into g ash-free dry weight by assuming that 1 g FW is equivalent to ~0.17 g ADW.

In southern areas such as the brackish lagoons on the east coast of Corsica in the Mediterranean (CASABIANCA & KIENER, 1969), the Ria de Arosa in NW Spain (IGLESIAS, 1981) and to a lesser extent also in Penpoul on the north coast of Brittany (SWEDMARK, 1958), Gobiidae are represented by largely resident populations without major fluctuations through the year. In contrast, gobiid populations in estuaries and coastal areas of NW Europe, where in winter water temperatures normally fall below 5°C, show marked seasonal variations in abundance. Due to the settling of a new year class, densities are highest in late summer or autumn (Table 10). During winter most individuals disappear and only a small proportion returns for breeding the following spring, when water temperatures again exceed 3°C. Although numbers decline due to mortality, the main cause for this phenomenon is believed to be offshore migration, either in relation to reproduction or to avoid low winter temperatures (*cf.* SWEDMARK, 1958; JONES & MILLER, 1966; HEALEY, 1971, 1972a; FONDS, 1973; HESTHAGEN, 1979; EVANS & TALLMARK, 1984). By fishing along the isobaths (every 10 m) in Gdansk Bay (Baltic), MORAWSKI (1978) observed 40% of all sand gobies to be concentrated at a depth of 70 to 80 m during winter. Remarkable is the observation that *P. minutus* is absent from the littoral zone of the inner Oslofjord, not only during winter at water temperatures below 3 to 5°C, but also in mid-summer at temperatures above 19°C (HESTHAGEN, 1977).

In Lake Grevelingen, however, the populations of *P. microps*, *P. minutus* and *G. niger* are landlocked from March to mid-October. Although water temperatures fall strongly towards the end of the year (Fig. 10) and part of the fish population migrates to the deeper parts of the lake, an exodus towards the North Sea has not been documented. Moreover, the decrease in numbers is constant throughout the period August to July of the next year (*cf.* Figs 3 and 4) and there are no indications of an increased rate of "mortality" during the months that the relatively small sluice would have made migration possible.

Compared with other areas, gobiid densities in Lake Grevelingen were relatively high (Table 10). According to the available literature, seasonal peak densities vary between 0.1 and 12.7 *P. minutus* per m^2. Curiously, highest densities were found in very shallow water with a minor tidal amplitude, *e.g.* in the Askö area in eastern Sweden, while in general *P. minutus* is supposed to live in deeper water than *P. microps* (*cf.* MUUS, 1967; FONDS, 1973; NELLBRING, 1986). In Lake Grevelingen too, the common goby is much more abundant in the littoral zone than is the sand goby.

For *P. microps*, densities range from 0.1 to 25.0 fishes per m^2. The score of Lake Grevelingen is relatively high, at least it was so in 1981 (Table 10).

Compared with the other two gobiids, the density of *G. niger* is generally two orders of magnitude lower (Table 10). Since we did not survey the relatively small surface area of submerged dike-foots, known to be inhabited by *G. niger* (WAARDENBURG *et al.*, 1984), the total number of black gobies in the lake may have been slightly underestimated.

According to SWEDMARK (1958) there is a negative relationship between the latitude and ultimate size of *P. minutus*. However, this is not confirmed by our data, since growth in Lake Grevelingen was, apart from being highly variable between years, largely similar to other NW European areas. A similar maximum length of 83 mm was found in Gullmar Fjord on the west coast of Sweden, while the greatest reported length (*viz.* 95 mm) stems from Penpoul on the north coast of Brittany in France (SWEDMARK, 1958). In the Dutch Wadden Sea, the mode of length distribution varied between 4 and 6 cm in the first year, but increased to 7 to 9 for animals still alive in the second year (FONDS, 1973). While approaching the completion of their first year of life, sand gobies in the inner Severn estuary reached a mean standard length of between 52 and 53 mm (CLARIDGE *et al.*, 1985), corresponding to a total length of approximately 59 mm, which is clearly higher than in Lake Grevelingen. It has been suggested that as a benefit of abundant food supply (due to eutrophication) in combination with high water temperatures, sand gobies in the inner Oslofjord attained average lengths of even 57 to 65 mm in their first year of life and 70 to 75 mm in their second (HESTHAGEN, 1977). Although growth may depend primarily on water temperature and food supply, the marked difference in growth rate between the 1980 and 1981 year class would appear to be due rather to intraspecific competition. Densities in 1980 were 15 times higher than in 1981, while water temperatures hardly differed (Fig. 10), and in the lake food is not believed to be limiting (see further on). Intraspecific competition for food and shelter observed in the bay goby *Lepidogobius* *lepidus* was thought to be an adaptive phenomenon to gain access to limiting resources (GROSSMAN, 1980). Hence, high densities will lead to an increase in stress and aggressive interactions, which in turn will affect growth adversely. The high density in Lake Grevelingen in early August 1980 can be illustrated best by the average surface area of only 25 cm^2 available to each sand goby, which had by then reached a mean body size of 4 cm! Similarly, the slow growth of *P. minutus* at Hvervenbukta in the inner Oslofjord, in comparison with a nearby bay, was also related to the higher population density (HESTHAGEN, 1977). Also the clearing and stocking experiments of KENNEDY & STRANGE (1986), carried out in an upland stream in northern Ireland, clearly confirm that inter- and intraspecific competition in juvenile salmon *Salmo salar* and trout *S. trutta* influences both survival and growth rates of under-yearling fish of both species.

Since in Lake Grevelingen juvenile *P. microps* grow up almost exclusively in the littoral zone, the absence of tidal movements combined with relatively high water temperatures (Fig. 10) could be responsible for the slightly better growth of the fish as compared with other areas (Table 11). However, the average final length of the adult common gobies appears to be more or less identical in all areas.

The theoretical mean final size ($\bar{L}_\infty$) of black gobies in the Oslofjord was estimated at 11.0 cm for females and 11.7 cm for males, while the largest animal measured 12.9 cm (NASH, 1984). In Lake Veere, O-group *G. niger* measured 3.6 to 4 cm in September/October. They attained an average length of 5 to 5.5 cm after one year (from May to May), 8 to 9 cm after 2 years, 10 to 11 cm after 3 years and 12.5 to 13 cm after 4 years (VAAS *et al.*, 1975). Animals kept in an aquarium even reached lengths of 15 to 16.7 cm. Growth in Lake Grevelingen was very similar, but apparently the fish disappear from natural waters before attaining maximum size.

According to VESEY & LANGFORD (1985), growth of *G. niger* in the Stanswood Bay on the south coast of England was faster than elsewhere because of raised water temperatures due to the cooling water discharge from the Fawley power station.

When the number of specimens and their mean lengths and weights were calculated back up to the pelagic stage, it appeared that 92 to 98% of the annual production in both gobiid populations was already attained in the period prior to the moment in late summer when the highest density was actually observed. As a consequence of the extrapolation procedures, production figures for Lake Grevelingen are much higher (roughly 10 times) than those found in areas with similar peak densities (Table 10). Since extrapolation was done on the basis of data derived from animals larger than 20 mm, and mortality is probably higher among the juveniles, the Lake Grevelingen production may even have been underestimated. According to

TABLE 11

Average length (in mm) of Pomatoschistus microps attained at the end of the first (L_0) and second (L_I) growing season in various areas and years in western Europe. In the case the standard length (SL) was measured this has been converted to total length (TL) on the basis of own data.

		L_0		L_I		
Area	*Year/Period*	*SL*	*TL*	*SL*	*TL*	*Reference*
Ythan estuary, E Scotland	1967-1968		33		53	HEALEY, 1972a
Balgzand, Dutch Wadden Sea	1975		36		47	VAN BEEK, 1976
	1976		37		47	VAN DER GAAG, 1977
Teign estuary, SW England	1976	31	38	43	51	FOUDA & MILLER, 1981
	1977	29	35	45	53	FOUDA & MILLER, 1981
Severn estuary, SW England	1972-1977	30-31*	36-38*	38-39*	45-46*	CLARIDGE *et al.*, 1985
Lake Grevelingen, SW Netherlands	1977		37		-	DE GRAAF, 1979
	1980		39		48	This study
	1981		39		51	This study
	1982		42		-	This study

* Modal length class

estimates from PIHL & ROSENBERG (1982), the production in a brown shrimp *Crangon crangon* population in the Gullmarsvik (western Sweden) would be reduced by 30 to 50% if specimens smaller than 12 mm were omitted due to the mesh selection of a 5 mm net. By changing towards a finer mesh size in the sampling gear, EVANS & TALLMARK (1984) were also able to improve the assessment of the annual shrimp production in the Kvarnbukten (western Sweden) by a factor 1.7.

Common to most areas, small crustaceans like Copepoda, Mysidacea, Isopoda, Amphipoda and Decapoda-Natantia (*i.e.* predominantly *Crangon crangon*) are the main food resource for *P. minutus* and *P. microps* (VAN BEEK, 1976; HESTHAGEN, 1977; MORAWSKI, 1978; ZANDER & HARTWIG, 1982; EVANS, 1983, 1984; CLARIDGE *et al.*, 1985; MÖLLER *et al.*, 1985), and Lake Grevelingen forms no exception. However, presumably due to local variations in availability of prey types, diet composition may differ considerably between years and nearby bays (*e.g.* PIHL, 1985). Thus, molluscs and particularly polychaetes have been found to contribute to the food of *P. minutus* as well (VAN BEEK, 1976; HESTHAGEN, 1977; MORAWSKI, 1978; EVANS, 1984) and occasionally also to the food of *P. microps* (ZANDER & HARTWIG, 1982), while Ostracoda are eaten by both gobiids (MÖLLER *et al.*, 1985). Juvenile *P. microps* and *P. minutus* from the shallow brackish Schlei Fjord (German Baltic coast) preyed largely on calanoids, harpacticoids and oligochaetes (SCHMIDT-MOSER & WESTPHAL, 1981). EVANS (1983) also observed that up to a size of approximately 30 mm, *P. minutus* fed merely on calanoid copepods, especially in July, while later on and with increasing length they included larger crustaceans and polychaetes.

We did not observe large differences in the food of the two species (*cf.* Fig. 9), but this may be partly because we analyzed only stomachs from areas deeper than 0.6 m. Therefore, it is likely that in the diet of *P. microps* in Lake Grevelingen, common food species from the littoral (*e.g. Corophium* sp. and *Crangon crangon*) have been underestimated.

Probably due to substantial eelgrass and *Chaetomorpha* sp. stands, covering at most 44 km^2 in 1978 (NIENHUIS, 1983), *Idotea chelipes*, and to a lesser extent, *Gammarus locusta* and *Praunus flexuosus* are locally abundant in the lake (GROENENDIJK, 1984). In 1978 the estimated annual production of *Praunus* was roughly 150 to 402 tons ADW and of *Idotea* 94 to 218 tons (A. FORTUIN, personal communication). Hence, at most 5 to 10% of this production was actually consumed by the gobiids. According to C. BAKKER (personal communication), the production of pelagic copepods in Lake Grevelingen during the period 1977 to 1980 amounted roughly to 25 (range 20 to 30) g ADW·m^{-2}·a^{-1}. Since the gobiids ate harpacticoids too, their annual cropping rate has to be less than 10% of the total copepods production.

In view of the estimated high annual production of the two species, the total consumption by their populations in Lake Grevelingen is also substantial. From our estimates, an average food conversion (growth/food) of 0.52 can be deduced (Table 8), which seems rather high in comparison with values given by PIHL (1985) (*viz.* an average P/C ratio for gobiids of 0.31; range 0.21 to 0.45). However, the net food conversion factor is age-dependent. According to our estimates the food conversion was approximately 0.4 (range 0.3 to 0.5) for young of the year, around 0.2 for new yearlings and less than 0.1 for ~1½-year-old gobies. Based on the figures given by PIHL (1985), the annual food consumption in Lake Grevelingen could be about twice as high. Even then food supply does not appear to be limiting for the gobiids in the lake.

In comparison with published values, the estimated annual mortality rates of *P. minutus* (~99.9%) and *P. microps* (~99.996%) in Lake Grevelingen appear to be rather high. In the western Wadden Sea and the adjacent North Sea coastal area, FONDS (1973) estimated, for *P. minutus*, a survival after one year (from October to October) varying from 5 to 9%, while 1 to 2% grew even 2 years old. Besides, he found mortality rates to be significantly lower in winter than in summer, which is not in agreement with our data. In the Ythan estuary (HEALEY, 1972b) and in the Oslofjord (HESTHAGEN, 1977), a similar life span of at most 23 months was found for *P. minutus*.

By examination of the annulus formation in scales, a maximum age of 21 to 26 months was estimated for *P. microps* from estuaries and shores of the Isle of Man and other parts of Great Britain. Most adult fishes, however, died in the second autumn of life at an age of 12 to 20 months (MILLER, 1975; FOUDA & MILLER, 1981).

In comparison with the 3-year-old *Gobius niger* found in Lake Grevelingen, a maximum of 4 year classes of this species were found together on the south coast of England (VESEY & LANGFORD,

1985) and even 5 in Lake Veere (VAAS *et al.*, 1975). In the Oslofjord the black goby also attained an age of at least 5 years (NASH, 1984).

In Lake Grevelingen the standing stocks of all Gobiidae together amounted to maximally 1.65 g FW·m^{-2} in September 1981. Other studies indicate that approximately 0.5 g·m^{-2} (even 1.4 g in 1980) of these fishes was consumed by plaice *Pleuronectes platessa* and flounder *Platichthys flesus* (DOORNBOS & TWISK, 1984) and 0.5 g·m^{-2} was taken by the great crested grebe *Podiceps cristatus* and red-breasted merganser *Mergus serrator* (DOORNBOS, 1984). Thus, at least 60% of the decline in gobiid biomass from late summer through the next spring could be accounted for by the predation by those flatfish and piscivorous bird species. Of the total gobiid production, however, only 17% was utilized by them.

Other important predators in Lake Grevelingen might be the cormorant *Phalacrocorax carbo* and the eel *Anguilla anguilla*. Although it may not be their main prey, cormorants are known to eat Gobiidae (*cf.* STEVEN, 1933; LACK, 1945). In the lake, cormorants as well as gobies (>20 mm) attain their seasonal peak densities during late summer to autumn. Particularly the bigger *P. minutus* would seem an appropriate prey when available in high densities, since cormorants feed in deeper water. Indeed, a highly significant ($P<0.001$; $N=10$) linear correlation was found between the numbers of cormorant-days over one year and the abundance of *P. minutus* (Fig. 11). Based on numbers and daily food requirements, a total fish consumption by cormorants of 0.4 g FW·m^{-2}·a^{-1} for 1980/1981 and of 0.26 g for 1981/1982 was estimated (DOORNBOS, 1984). Their diet, however, has not been examined.

Gobiids have also frequently been noticed in stomachs of eels from the lake. However, so far no quantitative stomach content analysis has been carried out. This is a serious shortcoming, since *A. anguilla* belongs to the dominant predacious fish in the lake. While the catches of plaice and flounder decreased steadily, the average annual commercial eel landings increased, for instance, from 69 tons during 1972 to 1977 to 85 tons (*i.e.* 0.8 g·m^{-2}) during 1979 to 1982 (DOORNBOS, 1982, 1985). Even herring *Clupea harengus* of 24 to 27 cm sometimes eat gobiid fish during part of the year (LUCASSEN, 1985). Other known consumers of gobiid fish in the lake are: dab *Limanda limanda*, turbot *Scophthalmus maximus*, brill *S. rhombus*, bull-rout *Myoxocephalus scorpius* and viviparous blenny *Zoarces viviparus*. However, their densities are rather low, as will be their predation impact. In the stagnant Lake Grevelingen, waders, including various species eating gobiid fish too, are much less numerous than in the former estuary. Nowadays, the Eurasian curlew *Numenius arquata* is, with only a few hundred individuals, one of the most abundant wader species in the lake. Particularly these birds will benefit from their size and bill length when foraging in shallow water along the shores, where they can catch shore crabs *Carcinus maenas* and common gobies (LAMBECK *et al.*, 1985).

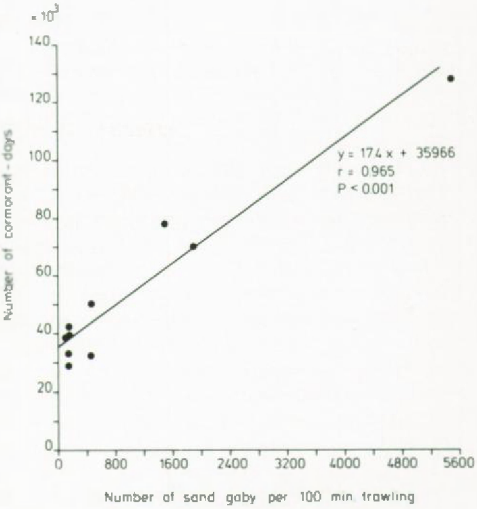


Fig. 11. Relationship between the number of cormorant-days (number of birds counted times number of days spent on the lake) over one year (from July through June) with the mean numbers of sand goby caught per 100 min. trawling over the preceding period January through December (see also legend of Fig. 12). One point for each of the years 1972 to 1982.

Hence, the main part of the decline in gobiid biomass from late summer onwards can be accounted for by predation. However, it is still unknown where the remaining 70 to 80% of the total gobiid fish production goes (produced predominantly by juveniles smaller than 20 mm).

After testing several hypotheses with respect to changes in water temperature, salinity, food supply and emigration to sea, HEALEY (1971, 1972a) supposed that the losses of *P. minutus* and *P. microps* in the Ythan estuary during winter might be explained by predation. However, he had no information on the diets of the potential predators. Evidence for predation was also given by MILLER (1975) while broadly discussing the causes of mortality in *P. microps* populations from the Silver Burn estuary (Isle of Man) and other parts of the British Isles.

In a steady-state energy flow model constructed for the Ythan estuary by BAIRD & MILNE (1981) the annual fish production was assessed at about 0.6 g C·m^{-2}·a^{-1}, of which piscivorous birds removed 0.46 g C·m^{-2} or 77%. Although this part of the food chain has been oversimplified, the high percentage (relative to other studies) bears a great resemblance to the effective transfer of energy observed in Lake Grevelingen. Hence, the abundant gobiid fishes must be considered to form an important link between the lower and higher trophic levels in the lake.

4.2. LONG-TERM VARIATION IN GOBIID ABUNDANCE

Ever since 1960, the estuaries in the SW Netherlands have been monitored with a 3 m beam trawl by the Delta Institute to determine possible changes in the fish fauna with particular reference to the ongoing hydraulic engineering works (*cf.* VAAS, 1979). Fig. 12 shows data for the catch per unit of effort of the Gobiidae compiled for the Grevelingen. However, it is possible that the *P. microps* samples are not representative, since fishing was done predominantly with a 10 x 10 mm net in an area deeper than 5 m.

Contrary to *P. minutus*, the population size of *P. microps* increased almost immediately after the enclosure in 1971. This suggests that littoral conditions became increasingly favourable for *P. microps*, which prefers the shallow (less than 1 m deep) waters of estuaries, fjords and bays (*cf.* JONES & MILLER, 1966; MUUS, 1967; HEALEY, 1972a; PIHL & ROSENBERG, 1982; NELLBRING, 1986). A marked decline in numbers followed during 1979 to 1980, the period coincident with an increase in *P. minutus*. Competition for food would appear to be an obvious explanation, since both species prey on rather similar organisms (see Chapter 3.7.). Also in competition experiments, EDLUND & MAGNHAGEN (1981) observed *P. microps* to be suppressed by *P. minutus* when they lived together. However, in Lake Grevelingen both populations occupy spatially largely separated habitats. Also changes in chlorinity in the course of time can hardly be suspected to have affected the breeding success of *P. microps* and *P. minutus* in the Grevelingen seriously, because estuarine species will be well adapted to fluctuating salinities.

According to FONDS (1973) the lethal temperatures for *P. microps* and *P. minutus* kept in sea water ($S \geq 8$) are about -1°C and -1.7°C, respectively. However, the condition of *P. microps* starts to deteriorate already at temperatures close to 0°C. Hence, this species may have suffered considerably from the severe winter of 1978/1979, when temperatures fell to 0°C in the 5 to 15 m water column and even below -1°C in the 0 to 5 m top layer (BAKKER & DE VRIES, 1984).

After the extremely severe winter of 1962/1963, *P. microps* had disappeared from the Dutch Wadden Sea and was not found again until the summer of 1965, while during that period the population size of *P. minutus* was estimated to be twice as high as in 1961 and 1962 (CREUTZBERG & FONDS, 1971). Also in the brackish Lake Veere the numbers of *P. microps* had decreased dramatically after the winter of 1962/1963, and the recovery took about 2 years. At the same time the population size of *P. minutus* was hardly affected (VAAS, 1970). These data support the hypothesis that the collapse of the *P. microps* population in Lake Grevelingen in 1979, followed by a retarded restoration, was mainly caused by the low water temperatures during the 1978/1979 winter.

It is unclear what may have caused the significant increase in the *P. minutus* population during the 1979 to 1981 period (Fig. 12). In 1978 manipulation experiments with the newly built sluice in the Brouwersdam resulted in a combined temperature-salinity stratification of the water masses (BAKKER & DE VRIES, 1984). In 1979 the sluice was open to the North Sea for the whole year, also resulting in a persistent stratification from the end of May to September (DE VOS *et al.*, 1980). Both stratifications have caused mass mortality among the benthic fauna below about 8 m (BANNINK *et al.*, 1984). As gobiid fish lay their eggs preferably inside or underneath bivalve shells (WHEELER, 1969, 1978; RUSSELL, 1976) *P. minutus*, breeding predominantly in 10 to 25 m deep water (FONDS, 1971, 1973), could have taken advantage of the sudden amount of vacant spawning places. This hypothesis is supported by the recently published results of the experiments carried out by NELLBRING (1986) in a shallow bay in the Baltic.

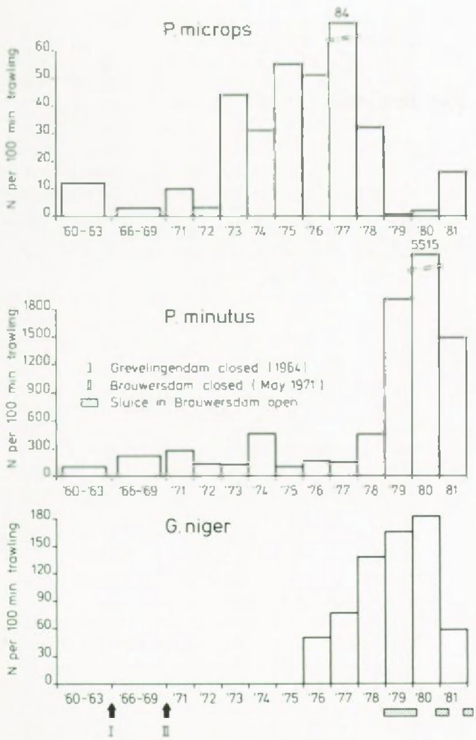


Fig. 12. Numbers (N) of *Pomatoschistus microps*, *P. minutus* and *Gobius niger* caught per 100 min. trawling in the deeper parts of the Grevelingen. Fishing was done by the Delta Institute with a 3 m beam trawl (without tickler chain) in an area deeper than 5 m. Catches are standardized for 10 x 10 mm mesh size.

He clearly demonstrated that a lack of suitable substrates limited the nesting of gobies in the bay. By offering artificial nest material, the density of breeding *P. minutus* increased 20 times compared with the natural situation. But how could *P. minutus* cope with the low oxygen conditions near the bottom of Lake Grevelingen, while the benthos died? Another explanation might be that large numbers of *P. minutus* have immigrated from the North Sea through the Brouwerssluice. An indication that immigration took place is that the painted goby *P. pictus* was observed in the lake for the first time in 1979 (DOORNBOS, 1981).

Gobius niger was first caught in 1976 (VAAS, 1979) and soon became abundant (Fig. 12). Apart from the decline in the catches in 1981, the population size appears to be increasing steadily.

5. REFERENCES

ANEER, G. & S. NELLBRING, 1977. A drop-trap investigation of the abundance of fish in very shallow water in the Askö area, northern Baltic proper. In: B.F. KEEGAN, P.O.CÉIDIGH & P.J.S. BOADEN. Biology of benthic organisms. Proc. 11th European Symposium in Marine Biology. Pergamon Press, Oxford: 21-30.

BAIRD, D. & H. MILNE, 1981. Energy flow in the Ythan estuary, Aberdeenshire, Scotland.—Estuar. coast. Shelf Sci. **13**: 455-472.

BAKKER, C. & I. DE VRIES, 1984. Phytoplankton- and nutrient dynamics in saline Lake Grevelingen (SW Netherlands) under different hydrodynamical conditions in 1978-1980.—Neth. J. Sea Res. **18**: 191-220.

BANNINK, B.A., J.H.M. VAN DER MEULEN & P.H. NIENHUIS, 1984. Lake Grevelingen: from an estuary to a saline lake. An introduction.—Neth. J. Sea Res. **18**: 179-190.

BEEK, F.A. VAN, 1976. Aantallen, groei, produktie en voedselopname van de zandgrondel (*P. minutus*) en de wadgrondel (*P. microps*) op het Balgzand. Interne Verslagen NIOZ, Texel, 1976-9: 1-53 (unpublished report).

BRAFIELD, A.E., 1985. Laboratory studies of energy budgets. In: P. TYTLER & P. CALOW. Fish energetics: new perspectives. Croom Helm Ltd, Beckenham, Kent: 257-281.

BRETT, J.R. & D.D. GROVES, 1979. Physiological energetics. In: W.S. HOAR, D.J. RANDALL & J.R. BRETT. Fish physiology. VIII. Bioenergetics and growth. Academic Press Inc., Orlando, Florida: 279-352.

CASABIANCA, M.-L. DE & A. KIENER, 1969. Gobiidés des étangs Corses: systématique, écologie, régime alimentaire et position dans les chaines trophiques.—Vie Milieu (Série A) **20**: 611-634.

CHAPMAN, D.W., 1978. Production. In: T.B. BAGENAL. Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford, IBP Handbook no. 3: 202-217.

CLARIDGE, P.N., M.W. HARDISTY, J.C. POTTER, & C.V. WILLIAMS, 1985. Abundance, life history and ligulosis in the gobies (Teleostei) of the inner Severn estuary.—J. mar. biol. Ass. U.K. **65**: 951-968.

COCHRAN, W.G., 1963. Sampling techniques. Wiley, London: 1-413.

CREUTZBERG, F. & M. FONDS, 1971. The seasonal variation in the distribution of some demersal fish species in the Dutch Wadden Sea.—Thalassia Jugoslavica **7**: 13-23.

DOORNBOS, G., 1981. Verwachtingen voor de ontwikkeling van de visstand in een zoute of zoete Grevelingen tegen de achtergrond van de veranderingen die zijn opgetreden in de visfauna in de periode

1960-1980. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke & Delta Dienst Rijkswaterstaat, Middelburg, Z 81 III 6: 1-28 (unpublished report).
——, 1982. Changes in the fish fauna of the former Grevelingen estuary, before and after the closure in 1971.—Hydrobiol. Bull. **16:** 279-283.
——, 1984. Piscivorous birds on the saline Lake Grevelingen, The Netherlands: abundance, prey selection and annual food consumption.—Neth. J. Sea Res. **18:** 457-479.
——, 1985. Vissen in de Grevelingen. In: P.H. NIENHUIS. Het Grevelingenmeer: van estuarium naar zoutwatermeer. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke & Natuur en Techniek, Maastricht: 130-145.
DOORNBOS, G. & F. TWISK, 1984. Density, growth and annual food consumption of plaice (*Pleuronectes platessa* L.) and flounder (*Platichthys flesus* (L.)) in Lake Grevelingen, The Netherlands.—Neth. J. Sea Res. **18:** 434-456.
DOORNBOS, G., F. TWISK & R.H. BOGAARDS, 1986. Kwantificering van vissen. ZOWEC III, Final Report. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke & Delta Dienst Rijkswaterstaat, Middelburg, Z 86 III 5: 1-190 (unpublished report).
EDLUND, A.-M. & C. MAGNHAGEN, 1981. Food segregation and consumption suppression in two coexisting fishes, *Pomatoschistus minutus* and *P. microps*: an experimental demonstration of competition.—Oikos **36:** 23-27.
ELLIOTT, J.M., 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size.—J. Anim. Ecol. **45:** 923-948.
ERENST, V. & P.J.F. DE GRAAF, 1983. Verspreiding, dichtheid en produktie van enkele kleine vissoorten in het litoraal van het Grevelingenmeer. Studentenverslag Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, D4-1983: 1-61 (unpublished report).
EVANS, S., 1983. Production, predation and food niche segregation in a marine shallow soft-bottom community.—Mar. Ecol. Prog. Ser. **10:** 147-157.
——, 1984. Energy budgets and predation impact of dominant epibenthic carnivores on a shallow soft bottom community at the Swedish west coast.—Estuar. coast. Shelf Sci. **18:** 651-672.
EVANS, S. & B. TALLMARK, 1979. A modified drop-net method for sampling mobile epifauna on marine shallow sandy bottoms.—Holarct. Ecol. **2:** 58-64.
——, 1984. Seasonal dynamics of small vagile predators on a marine shallow soft bottom.—Holarct. Ecol. **7:** 138-148.
FONDS, M., 1970. Remarks on the rearing of gobies (*Pomatoschistus minutus* and *P. lozanoi*) for experimental purposes.—Helgoländer wiss. Meeresunters. **20:** 620-628.
——, 1971. The seasonal abundance and vertebral variation of *Pomatoschistus minutus minutus* and *lozanoi* (Gobiidae) in the Dutch Wadden Sea.—Vie Milieu (Suppl.) **22:** 393-408.
——, 1973. Sand gobies in the Dutch Wadden Sea (*Pomatoschistus*, Gobiidae, Pisces).—Neth. J. Sea Res. **6:** 417-478.
FONDS, M. & C. VELDHUIS, 1973. The oxygen consumption of four *Pomatoschistus* species (Pisces, Gobiidae) in relation to water temperature.—Neth. J. Sea Res. **7:** 376-386.
FONDS, M., R. CRONIE, D. VETHAAK & P. VAN DER PUYL, 1985. Laboratory measurements of maximum daily food intake, growth and oxygen consumption of plaice (*Pleuronectus platessa*) and flounder (*Platichthys flesus*), in relation to water temperature and the size of the fish. ICES Demersal Fish Committee C.M. 1985/G:54: 1-7.
FOUDA, M.M. & P.J. MILLER, 1981. Age and growth of the common goby, *Pomatoschistus microps*, on the south coast of England.—Estuar. coast. Shelf Sci. **12:** 121-129.
GAAG, M. VAN DER, 1977. Aantallen, verdeling, groei en voedselopname van twee grondelsoorten op het Balgzand in 1975 en 1976. Interne Verslagen NIOZ, Texel, 1977-9: 1-80 (unpublished report).
GLAZENBURG, A.K., 1982. Interspecifieke konkurrentie als mogelijke verklaring voor aantalsfluktuaties van twee grondelsoorten in de Grevelingen (*Pomatoschistus minutus* en *P. microps*). Studentenverslag Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, D6-1982: 1-36 (unpublished report).
GRAAF, U.H. DE, 1979. Enkele kleine vissoorten in de ondiepe delen van het Grevelingenmeer: een schatting van hun aantal, biomassa en productie. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, Rapp. en Versl. 1979-1: 1-49 (unpublished report).
GROENENDIJK, A.M., 1984. Consumption of eelgrass (*Zostera marina* L.) by the isopod *Idotea chelipes* (Pallas) in Lake Grevelingen, after the growing season.—Neth. J. Sea Res. **18:** 384-394.
GROSSMAN, G.D., 1980. Food, fights, and burrows: the adaptive significance of intraspecific aggression in the bay goby (Pisces: Gobiidae).—Oecologia **45:** 261-266.
HEALEY, M.C., 1971. The distribution and abundance of sand gobies, *Gobius minutus*, in the Ythan estuary.—J. Zool., Lond. **163:** 177-229.
——, 1972a. On the population ecology of the common goby in the Ythan estuary.—J. nat. Hist. **6:** 133-145.
——, 1972b. Bioenergetics of a sand goby (*Gobius minutus*) population.—J. Fish. Res. Bd Can. **29:** 187-194.
HESTHAGEN, I.H., 1977. Migrations, breeding, and growth in *Pomatoschistus minutus* (Pallas) (Pisces, Gobiidae) in Oslofjorden, Norway.—Sarsia **63:** 17-26.
——, 1979. Temperature selection and avoidance in the sand goby, *Pomatoschistus minutus* (Pallas), collected at different seasons.—Env. Biol. Fish. **4:** 369-377.
IGLESIAS, J., 1981. Spatial and temporal changes in the demersal fish community of the Ria de Arosa (NW Spain).—Mar. Biol. **65:** 199-208.
JONES, D. & P.J. MILLER, 1966. Seasonal migrations of

the common goby, *Pomatoschistus microps* (Krøyer), in Morecambe Bay and elsewhere.—Hydrobiologia **27**: 515-528.

KENNEDY, G.J.A. & C.D. STRANGE, 1986. The effects of intra- and interspecific competition on the survival and growth of stocked juvenile Atlantic salmon, *Salmo salar* L., and resident trout, *Salmo trutta* L., in an upland stream.—J. Fish. Biol. **28**: 479-489.

KING, T.A., J.C. WILLIAMS, W.D. DAVIES & W.L. SHELTON, 1981. Fixed versus random sampling of fishes in a large reservoir.—Trans. Amer. Fish. Soc. **110**: 563-568.

KUIPERS, B.R., 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*).—Neth. J. Sea Res. **9**: 69-85.

LACK, D., 1945. The ecology of closely related species with special reference to cormorant (*Phalacrocorax carbo*) and shag (*P. aristotelis*).—J. Anim. Ecol. **14**: 12-16.

LAMBECK, R.H.D., G. DOORNBOS & J. BEIJERSBERGEN, 1985. Komen, gaan of blijven. Variaties in de vogelstand.—Natuur Tech. **53**: 490-505.

LUCASSEN, W.G.H., 1985. Een vergelijkend onderzoek naar het voedsel van vier pelagische vissoorten in het Grevelingenmeer. Studentenverslag Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, D5-1985: 1-61 (unpublished report).

MCLUSKY, D.S, 1981. The estuarine ecosystem. Blackie, Glasgow: 1-150.

MILLER, P.J., 1975. Age-structure and life-span in the common goby, *Pomatoschistus microps*.—J. Zool., Lond. **177**: 425-448.

MÖLLER, P., L. PIHL & R. ROSENBERG, 1985. Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats.—Mar. Ecol. Prog. Ser. **27**: 109-121.

MORAWSKI, M.S., 1978. Winter feeding of the sand goby (*Pomatoschistus minutus* Pallas) in relation to the depth in Gdansk Bay.—Kieler Meeresforsch. (Sonderh.) **4**: 122-127.

MUUS, B.J., 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone.—Meddr Danm. Fisk.- og Havunders. (N.S.) **5**: 1-316.

NASH, R.D.M., 1984. Aspects of the biology of the black goby, *Gobius niger* L., in Oslofjorden, Norway.—Sarsia **69**: 55-61.

NELLBRING, S., 1986. A quantitative and experimental study of goby (*Pomatoschistus* spp.) nests on a shallow soft bottom, northern Baltic proper.—Ophelia **25**: 15-23.

NIENHUIS, P.H., 1978a. An ecosystem study in Lake Grevelingen, a former estuary in the SW Netherlands.—Kieler Meeresforsch. (Sonderh.) **4**: 247-255.

——, 1978b. Lake Grevelingen: a case study of ecosystem changes in a closed estuary.—Hydrobiol. Bull. **12**: 246-259.

——, 1983. Temporal and spatial patterns of eelgrass (*Zostera marina* L.) in a former estuary in The Netherlands, dominated by human activities.—Mar. Technol. Soc. J. **17**: 69-77.

PIHL, L., 1985. Food, selection and consumption of mobile epibenthic fauna in shallow marine areas.—Mar. Ecol. Prog. Ser. **22**: 169-179.

PIHL, L. & R. ROSENBERG, 1982. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden.—J. exp. mar. Biol. Ecol. **57**: 273-301.

RUSSELL, F.S., 1976. The eggs and planktonic stages of British marine fishes. Academic Press, London: 253-281.

SAMPFORD, M.R., 1962. An introduction to sampling theory. Oliver & Boyd, London: 1-292.

SCHMIDT-MOSER, R. & D. WESTPHAL, 1981. Predation of *Pomatoschistus microps* Krøyer and *P. minutus* Pallas (Gobiidae, Pisces) on macro- and meiofauna in the brackish fjord Schlei.—Kieler Meeresforsch. (Sonderh.) **5**: 471-478.

SOOFIANI, N.M. & A.D. HAWKINS, 1985. Field studies of energy budgets. In: P. TYTLER & P. CALOW. Fish energetics: new perspectives. Croom Helm Ltd, Beckenham, Kent: 283-307.

STEVEN, G.A., 1933. The food consumed by shags and cormorants around the shores of Cornwall (England).—J. mar. biol. Ass. U.K. **19**: 277-292.

SWEDMARK, M., 1958. Sur la variation géographique de *Gobius minutus* Pallas. I. Biologie et croissance.—Archs Zool. exp. gen. Notes Rev. **95**: 32-51.

VAAS, K.F., 1970. Studies on the fish fauna of the newly created lake near Veere, with special emphasis on the plaice (*Pleuronectes platessa*).—Neth. J. Sea Res. **5**: 50-95.

——, 1979. Studies on the fish fauna of an estuary in the S.W. Netherlands, before and after its change into the stagnant, saline, Lake Grevelingen.—Hydrobiol. Bull. **13**: 177-188.

VAAS, K.F., A.G. VLASBLOM & P. DE KOEIJER, 1975. Studies on the black goby (*Gobius niger*, Gobiidae, Pisces) in the Veerse Meer, SW Netherlands.—Neth. J. Sea Res. **9**: 56-68.

VESEY, G. & T.E. LANGFORD, 1985. The biology of the black goby, *Gobius niger* L. in an English south-coast bay.—J. Fish Biol. **27**: 417-429.

VLAS, J. DE, 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey.—Neth. J. Sea Res. **13**: 117-153.

VOS, C.P. DE, J.S.L. VINK, B.A. BANNINK & J. LEENTVAAR, 1980. Water quality impacts of exchanging water between sea and a closed estuary.—Prog. Wat. Tech. **13**: 271-285.

WAARDENBURG, H.W., A.J.M. MEIJER, R.J.L. PHILLIPART & A.C. VAN BEEK, 1984. The hard bottom biocoenoses and the fish fauna of Lake Grevelingen, and their reactions to changes in the aquatic environment.—Wat. Sci. Tech. **16**: 677-686.

WHEELER, A., 1969. The fishes of the British Isles and north-west Europe. Macmillan, London: 410-430.

——, 1978. Key to the fishes of northern Europe. Frederick Warne, London: 303-319.

WINBERG, G.C., 1956. Rate of metabolism and food re-

quirements of fishes.—Fish. Res. Bd Can. (Transl. Ser.) **194** (1960): 1-202.
ZANDER, C.D. & E. HARTWIG, 1982. On the biology and food of small-sized fish from North and Baltic Sea areas. IV. Investigations on an eulittoral mud flat at Sylt Island.—Helgoländer Meeresunters. **35**: 47-63.

(received 11-12-1986)

CHAPTER 6
HOOFDSTUK

Netherlands Journal of Sea Research
18 (3/4): 457-479 (1984)

PISCIVOROUS BIRDS ON THE SALINE LAKE GREVELINGEN, THE NETHERLANDS: ABUNDANCE, PREY SELECTION AND ANNUAL FOOD CONSUMPTION*

by

G. DOORNBOS

Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA Yerseke, The Netherlands

CONTENTS

1. INTRODUCTION

By constructing the Grevelingendam on the east side finished in 1964 and the closure of the Brouwershavensche Gat in 1971 on the west side of the former estuary, a stagnant saline Lake Grevelingen (108 km^2) has been created (Fig. 1). After the contact with the North Sea had been broken the chlorinity in the lake decreased steadily, from 17 to less than 13‰ Cl^- (NIENHUIS, 1978). In December 1978, the Brouwerssluice, built to exchange water from the lake with seawater, became operative. From then onwards the chloride concentration stabilized at about 16‰ Cl^- (BANNINK *et al.*, 1984).

The closure has resulted in a major change in the abundance of fish-eating birds. Before 1971, the maximum number of Great Crested Grebe *Podiceps cristatus* amounted to only 80 birds (WOLFF, 1967). After the closure, the peak numbers, reached during winter or early spring, increased rapidly from 2100 in 1972 to 9400 birds in 1975 (SAEIJS & BAP-

* Communication nr. 298 of the Delta Institute for Hydrobiological Research, Yerseke, The Netherlands

TIST, 1976a, 1976b). Considering that the size of the northwestern European population, breeding in Sweden, Norway, Denmark, northern Germany and The Netherlands, is estimated at about 9000 pairs (LEYS & DE WILDE, 1971), Lake Grevelingen has become one of the main areas visited by migrating grebes.

In the former estuary, a maximum of 91 Red-breasted Mergansers *Mergus serrator* was present. After the closure, the number increased from 450 during the 1971/1972 winter to 1100 birds in April 1975. Similar developments hold for the Cormorant *Phalacrocorax carbo*. Only 2 specimens were observed before 1971, while the autumn peak increased from 325 in 1972 to 640 birds in 1974. The maximum number of Grey Heron *Ardea cinerea*, the least prominent of the piscivorous species, increased from about 20 (before 1971) to 170 specimens in September 1973 (WOLFF, 1967; WOLFF *et al.*, 1976; SAEIJS & BAPTIST, 1976a).

The major increase in the number of fish-eating birds has been related to the much higher transparency of the water (WOLFF *et al.*, 1976; SAEIJS & BAPTIST, 1976a, 1977). Secchi-disc values of 2 to 9 m were measured in the lake, while those previously in the estuary were only 0.5 to 2.5 m (NIENHUIS, 1978; BANNINK *et al.*, 1984).

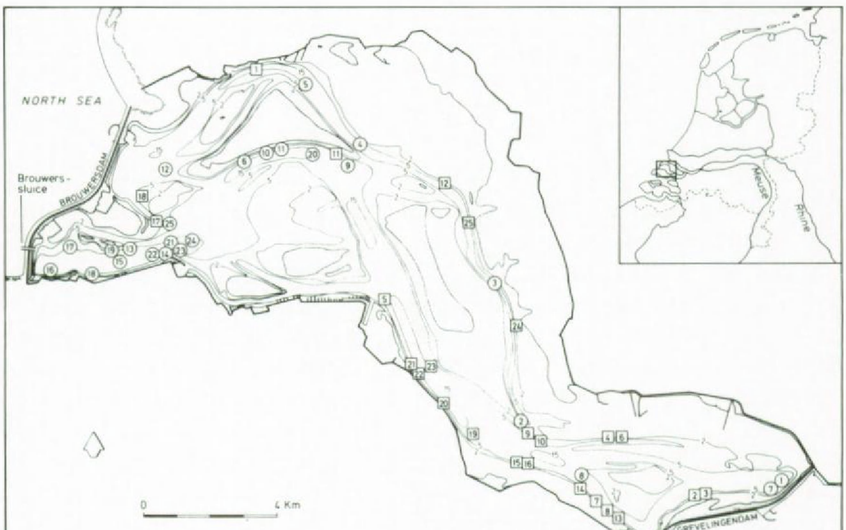


Fig. 1. Map of Lake Grevelingen (SW Netherlands). Depth contours in meters. Permanently dry areas shaded. Sampling places of individual Great Crested Grebes (○) and Red-breasted Mergansers (□) are indicated. Numbers refer to individuals in Appendix 2.

Almost nothing was known about the impact of the fish-eating birds on the fish populations in Lake Grevelingen. However, the sharp fall in the population size of the gobiid fish during every autumn and winter in the absence of piscivorous fish in the lake has been conceived to be an indication of heavy predation by birds (DOORNBOS, 1981). It appeared that only 1-2% of the O-group animals present in August survived the winter period.

The aim of the present study is to gain more insight into the predator-prey relationship between these birds and the fish. The major questions are: what do the birds prey on and what share of the annual production of the various fish species do they consume?

Acknowledgements.—This study was part of the ZOWEC project (saline water ecology) and financed by the Deltadienst of Rijkswaterstaat. I am much indebted to all of those who assisted in the field and in the laboratory, as well as those who gave valuable advice and support. I especially want to mention: M.C. Mol of Staatsbosbeheer, P.L. Meininger of the Deltadienst, W.J.L. Robër and P. de Koeijer of the research vessel "Maris Stella", Dr A.G. Vlasblom and J.J. Guerand of the biomathematical department, Mrs M.J. van Leerdam-de Dreu who did the typing, A.A. Bolsius for making the final drawings and Mrs P. Pollen-Lindeboom for correcting the English text. R.H. Bogaards assisted in the field and did most of the laboratory analyses, while Dr F.H.M. Borgsteede of the Centraal Diergeneeskundig Instituut identified the intestinal worms of the birds. Dr N. Daan and R.H.D. Lambeck gave comments on the first draft of the manuscript.

2. MATERIAL AND METHODS

Based on the biweekly bird counts of Staatsbosbeheer, started in the Grevelingen in 1971 (SAEIJS & BAPTIST, 1976a, 1978), the population development of the piscivorous birds in the lake during 1971 to 1982 has been derived. From these data, the annual number of bird-days and the total food consumption has also been estimated.

During each month in the period December 1981 through March 1982, 6 to 7 Great Crested Grebes and Red-breasted Mergansers, the two most numerous fish-eating bird species, were shot from a small boat at their most prominent foraging areas at that moment. Mergansers were usually shot in the eastern part of the lake and grebes in the western, particularly during February and March (Fig. 1). In total, 25 individuals of the two species were collected. After measuring, weighing, aging and sexing, the gullet and stomach contents were removed and preserved in a 70% alcohol solution.

Intact food items could be identified directly. The remains of the more or less digested preys were determined by the revealing species specific otoliths (fish) or claws (shrimps).

Using the relationship between the fish length and the size of the otoliths, the length of the fish consumed by the birds can be reconstructed by measuring the length of the otoliths in the stomach contents (*e.g.* POPOVA, 1978; DOORNBOS, 1979). Otolith and claw lengths were measured using a dissecting microscope with a micrometer eyepiece. The types of measurements taken are indicated in Fig. 2. Subsequently the length of the fish has been converted into fresh weight on basis of an average length-weight relationship. To construct the various correlation diagrams required, approximately 100 specimens of each of the main food species were measured (Fig. 2; Table 1). Discrimination between

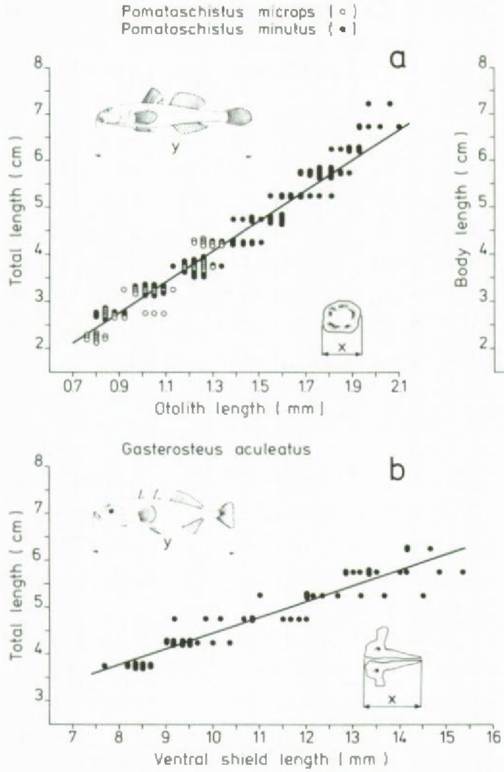


Fig. 2. a. Relationship between otolith length and fish length in *Pomatoschistus microps* (○) and *P. minutus* (●). b. Relationship between ventral shield length and fish length in *Gasterosteus aculeatus*. c. Relationship between claw length and body length in *Crangon crangon*. For regression-equations see Table 1.

TABLE 1

Relationships between body length (L in cm) and fresh weight (W in g) and between length (X in mm) of otolith, or ventral shield, or claw, and body length (L in cm) for the most important prey species. Approximately 100 individuals per species were measured.

Species	*Size range (cm)*	$W = a L^b$	*Object of determination*	$L = m X + n$
Pomatoschistus microps	2- 5	$W = 0.00822\ L^{3.082}$	otolith	$L = 3.44\ X - 0.36$
Pomatoschistus minutus	2- 8	$W = 0.00497\ L^{3.281}$	otolith	$L = 3.37\ X - 0.20$
P. microps + *P. minutus*	2- 8	$W = 0.00798\ L^{3.025}$	otolith	$L = 3.27\ X - 0.18$
Gobius niger	2-13	$W = 0.00766\ L^{3.241}$	otolith	$L = 2.10\ X + 0.64$
Atherina presbyter	5-14	$W = 0.00355\ L^{3.298}$	otolith	$L = 2.80\ X + 0.01$
Clupea harengus	7-18	$W = 0.00861\ L^{2.922}$	otolith	$L = 4.72\ X - 0.07$
Sprattus sprattus	6-14	$W = 0.00237\ L^{3.542}$	otolith	$L = 6.80\ X - 0.89$
Gasterosteus aculeatus	2- 7	$W = 0.01157\ L^{2.815}$	ventral shield	$L = 3.38\ X + 1.07$
Crangon crangon	1- 8	$W = 0.00699\ L^{3.326}$	claw	$L = 1.60\ X + 0.73$

the otoliths of the closely related common goby *Pomatoschistus microps* and sand goby *P. minutus* was not possible, although the former is generally the smaller of the two (Fig. 2a). In addition, the otoliths of the black goby *Gobius niger* smaller than ±5 cm were difficult to discriminate from those of the other gobiid species. In the case of doubt they were treated as being *P. microps* or *P. minutus*. Since the otoliths of the three-spined stickleback *Gasterosteus aculeatus* are very small, their spiny ventral shields (basipterygium) proved to be more useful (Fig. 2b). In case of the brown shrimp *Crangon crangon*, body length was related with the claw (dactylus) length (Fig. 2c). The number of otoliths and claws of a 5 mm length class found in the stomach contents of a bird was divided by two to obtain the number of fishes or shrimps eaten, respectively (odd numbers were rounded up).

In addition to the food items, all other items recognized in the gullets and stomachs were identified as well. A brief enumeration is given in Appendix 1.

By extracting the dried (at 80°C) carcasses three times with sufficient fresh petroleum ether (boiling range 40-60°C), the fat content of the individual birds was obtained.

3. RESULTS

3.1. LONG-TERM DEVELOPMENTS IN THE NUMBER OF BIRDS

After a rapid increase directly after the closure of the estuary the maximum number of wintering grebes stabilized between 1975 and 1978, with peak values reaching 7000 to 10 000 birds in early spring (Fig. 3a).

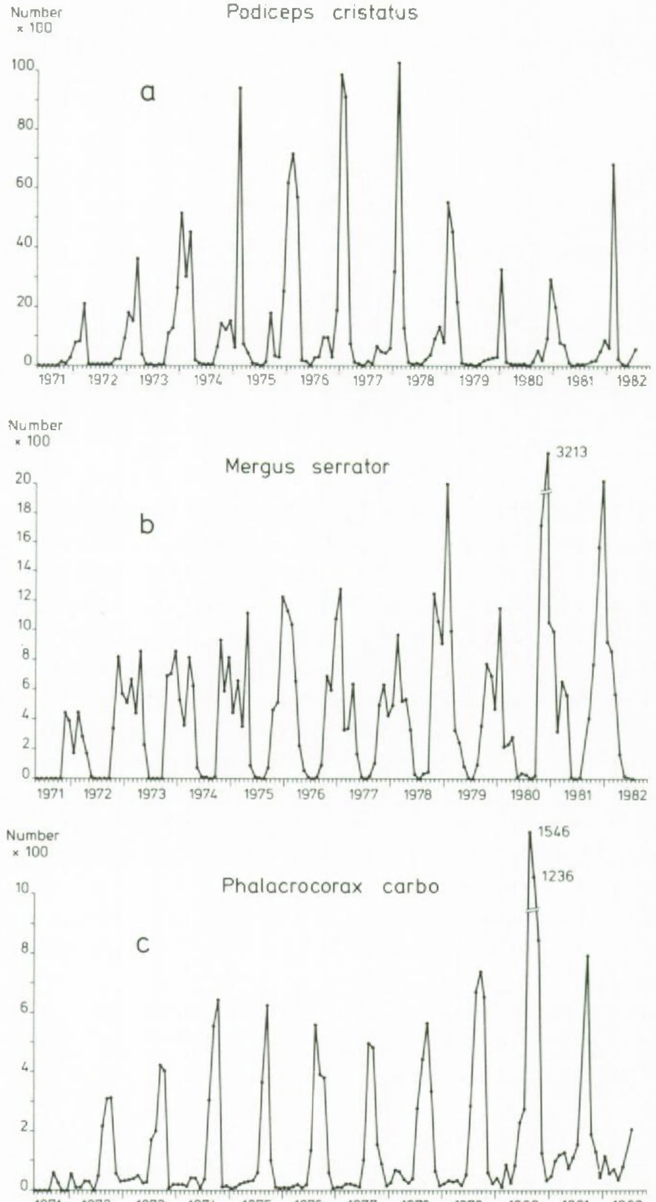


Fig. 3. Monthly peak numbers of: a. Great Crested Grebe *Podiceps cristatus*, b. Red-breasted Merganser *Mergus serrator* and c. Cormorant *Phalacrocorax carbo*. Data obtained from Staatsbosbeheer.

TABLE 2

Seasonal (1 July-30 June) number of bird-days (B-D) per species, and the estimated annual food consumption (F in metric tons fresh weight) in the period 1971 to 1982.

Period	*Great Crested Grebe*		*Red-breasted Merganser*		*Cormorant*		*Grey Heron*		*Total*
	B-D $(\cdot 10^3)$	*F* *(tons)*	*B-D* $(\cdot 10^3)$	*F* *(tons)*	*B-D* $(\cdot 10^3)$	*F* *(tons)*	*B-D* $(\cdot 10^3)$	*F* *(tons)*	*F* *(tons)*
71-72	91.3	18.7	44.6	9.0	4.6	1.7	2.4	0.6	30.0
72-73	179.7	36.8	103.1	20.8	29.2	10.7	8.0	2.0	70.3
73-74	368.3	75.5	98.6	19.9	33.5	12.3	7.3	1.8	109.5
74-75	294.5	60.4	127.5	25.8	32.5	12.0	2.5	0.6	98.8
75-76	561.4	115.1	120.4	24.3	38.8	14.3	4.1	1.0	154.7
76-77	515.7	105.7	122.9	24.8	39.6	14.6	2.9	0.7	145.8
77-78	456.1	93.5	111.2	22.5	42.6	15.7	2.3	0.6	132.3
78-79	396.4	81.3	186.8	37.7	50.2	18.5	2.0	0.5	138.0
79-80	112.1	23.0	108.4	21.9	70.3	25.9	3.1	0.8	71.6
80-81	215.8	44.2	209.3	42.2	128.0	47.1	4.3	1.1	134.6
81-82	227.2	46.6	194.2	39.2	77.8	28.6	1.9	0.5	114.9

Subsequently, the peak declined again to less than 3000 individuals in 1980/1981. However, according to the number of bird-days spent in the area by grebes, the decline in the total visiting time already started in 1976/1977 and reached its lowest value in 1979/1980 (Table 2).

In contrast to the grebes, the presence of the Red-breasted Merganser still increases, although less rapidly (Fig. 3b; Table 2). During 1978 to 1982, winter peaks reaching 2000 birds or more were not uncommon.

The number of Cormorants which predominantly visit the area from July through October has also increased (Fig. 3c; Table 2). Except in August 1980, the annual peak numbers appear fairly stable, fluctuating from 500 to 800 specimens.

The Grey Heron is the least numerous of all (Table 2). Maximum numbers were generally observed in September and ranged between 23 (1971) and 169 (1973) individuals.

3.2. SPECIES SELECTION

From the contents of the gullets and stomachs of the 25 grebes shot a total of 1208 prey items could be reconstructed, 93% of which were small fishes and 7% brown shrimps (Table 3). Among these, gobiid fish, *i.e. Pomatoschistus microps, P. minutus* and *Gobius niger*, were predominant, both in number (88%) and biomass (61%). Small pelagic fish such as the three-spined stickleback *Gasterosteus aculeatus*, sprat *Sprattus sprattus* and sand-smelt *Atherina presbyter* were of minor importance. Because of

TABLE 3

Reconstructed number (N) and fresh weight (W in g) of prey of various types in the stomach contents of 25 Great Crested Grebes and 25 Red-breasted Mergansers (n.i. = not identified, * = pro forma weight).

Prey species	*Great Crested Grebe*				*Red-breasted Merganser*			
	N	%	*W*	%	*N*	%	*W*	%
Fish								
Gobiidae	1062	87.9	901	60.8	662	61.8	600	59.2
Clupea harengus	38	3.1	316	21.3	–	–	–	–
Sprattus sprattus	16	1.3	105	7.1	–	–	–	–
Atherina presbyter	8	0.7	9	0.6	4	0.4	3	0.3
Gasterosteus aculeatus	1	0.1	1	0.1	50	4.7	61	6.0
Anguilla anguilla	–	–	–	–	12	1.1	33	3.3
Syngnathus rostellatus	–	–	–	–	1	0.1	1	0.1
Merlangius merlangus	1	0.1	30	2.0	–	–	–	–
Gadus sp.	1	0.1	30*	2.0	–	–	–	–
n.i.	–	–	–	–	2	0.2	10*	1.0
total fish	1127	93.3	1392	93.9	731	68.3	708	69.9
Crustaceans								
Crangon crangon	80	6.6	88	6.0	333	31.1	284	28.0
Carcinus maenas	1	0.1	2	0.1	6	0.6	21	2.1
total crustaceans	81	6.7	90	6.1	339	31.7	305	30.1
Total all prey	1208	100	1482	100	1070	100	1013	100

their relatively high individual weight, the few herring *Clupea harengus* taken by the grebes accounted for 21% of the total amount of food in weight.

The stomachs of the mergansers revealed the remains of 731 (68%) fishes and 339 crustaceans (Table 3), of which gobiid fish (62%) and the brown shrimp *Crangon crangon* (31%) were the dominant prey species. The crustaceans accounted for a much larger proportion of the food in weight (30%) than in the grebes. Herring and sprat were not found at all, while other prey, *i.e.* sand-smelt, stickleback, eel *Anguilla anguilla* and Nilsson's pipefish *Syngnathus rostellatus*, were insignificant.

In terms of numbers, the percentage of gobiid fish in the stomachs of the birds largely reflects the (demersal) fish fauna of the lake, as indicated by the beam trawl catches during September to October 1981 which consisted for 97% of Gobiidae (Fig. 4). However, in terms of weight the share of these small fishes was only 44%. Due to the similarity in the otoliths there is no direct evidence of selection on a particular gobiid species.

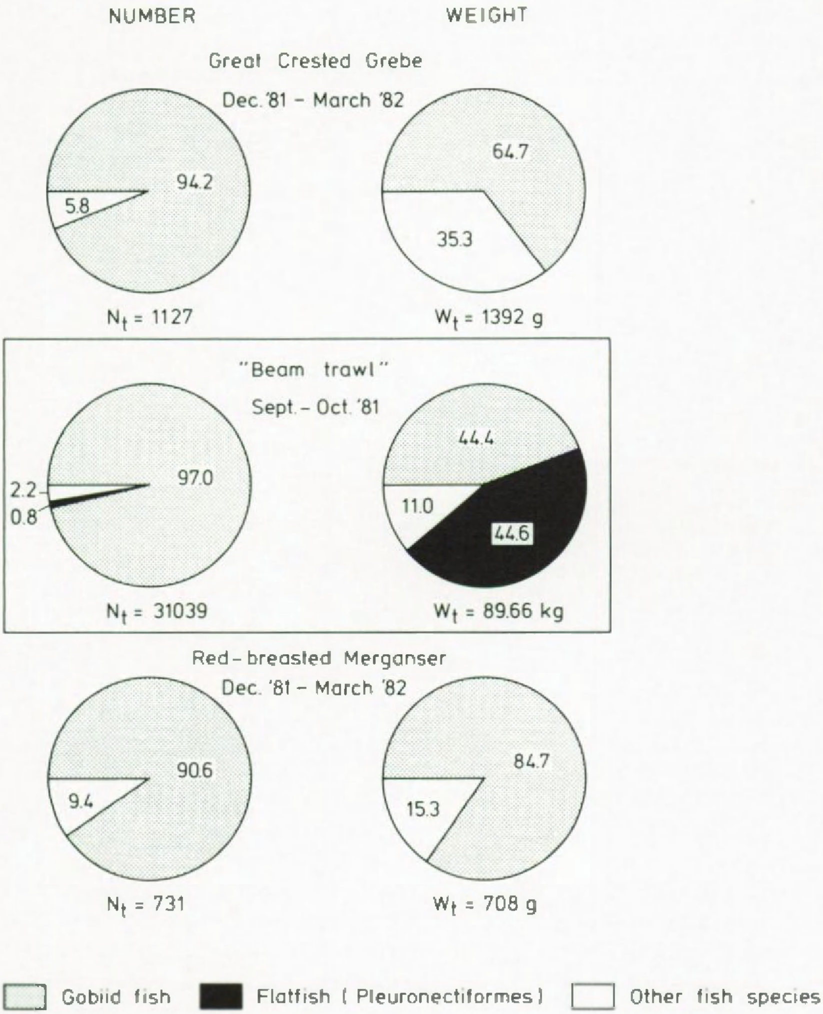


Fig. 4. Comparison of number and biomass percentages of the main fish species (excluding crustaceans) in the stomach contents of the grebes and mergansers with those in beam trawl catches during September and October 1981.

3.3. SIZE SELECTION

The fish taken by the grebes and mergansers were generally small; approximately 95% ranged between 2 and 7 cm. Only the few sprat and herring consumed by the grebes were bigger, an average of 9.1 cm

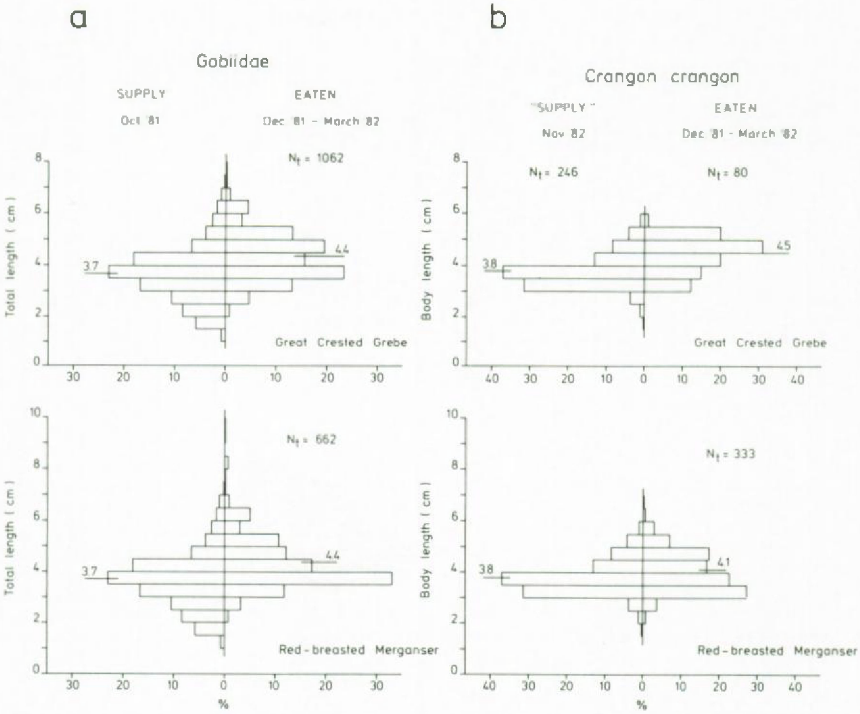


Fig. 5. Comparison of length-frequency distribution of: a. Gobiidae and b. *Crangon crangon* eaten by grebes and mergansers with that of the fishes and shrimps in the lake. The average lengths are indicated by a horizontal bar.

(range 6 to 11.5 cm) and 10.1 cm (range 7 to 15 cm), respectively, and the eel eaten by the mergansers ranged from 10 to 18.5 cm.

When comparing the length-frequency distribution of Gobiidae in the stomachs with that found in the lake, it appears that the birds selected the larger ones (Fig. 5a). The reconstructed length of the fish from the stomachs was on the average 7 mm longer than those in the lake. Unfortunately, no data on *Crangon crangon* are available for the lake in 1981, but assuming the same size distribution for 1981 as in November 1982, the grebes showed a tendency to select the larger specimens, and certainly larger specimens than the mergansers (Fig. 5b).

3.4. SEASONAL PATTERNS IN QUALITATIVE AND QUANTITATIVE STOMACH CONTENTS

Although almost all birds were shot at about the same time of the day, the December and January birds contained significantly more prey specimens ($p < 0.01$) than the February and March ones (Fig. 6a and b). Particularly the number of Gobiidae in the stomachs decreased sharply in the course of the winter season. For the Great Crested Grebe the decline of gobiid fish in the diet was (partly) compensated by a higher consumption of relatively heavier and fattier clupeid fish (Fig. 6c). In case of the Red-breasted Merganser no significant compensation could be observed (Fig. 6d). On the contrary, in the course of the winter season the mergansers changed to smaller sized shrimps (Fig. 7). No shift in the average length of the consumed gobiid fish was observed.

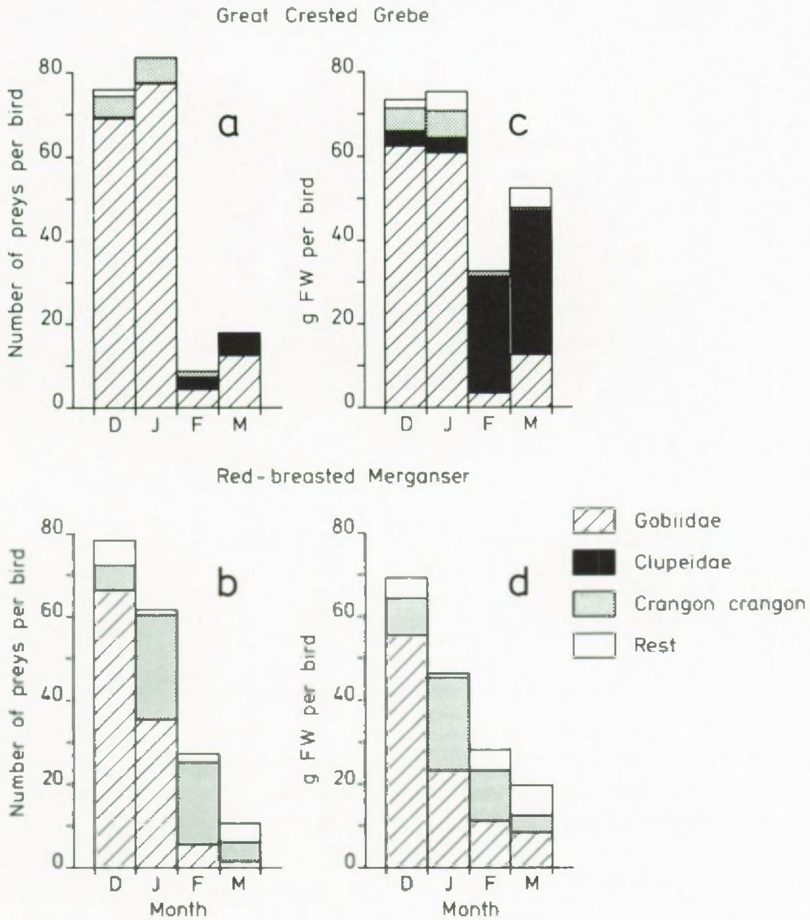


Fig. 6. Mean stomach content per bird during December to March, based on the reconstructed numbers and weights of the prey.

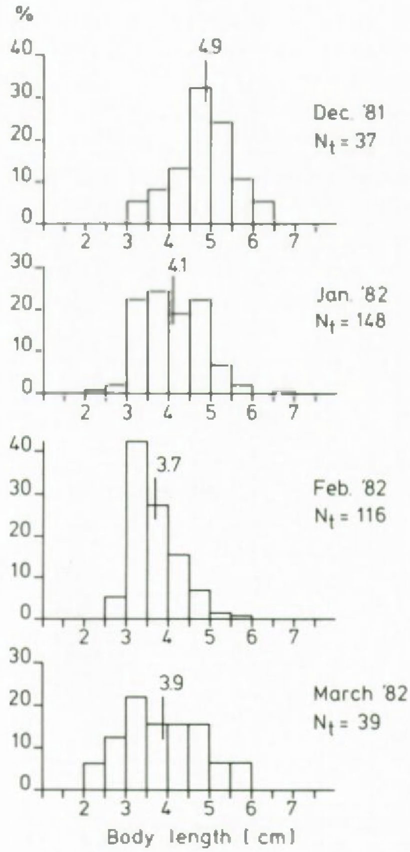


Fig. 7. Monthly change in length-frequency distribution of *Crangon crangon* in the stomachs of the Red-breasted Merganser. The average lengths are indicated by a vertical bar. The size of the consumed shrimps is significantly larger ($p < 0.001$) in December than in the subsequent months.

3.5. FOOD CONSUMPTION

The average daily food consumption (F in g) of grebes and mergansers in the wild was estimated from their live weights (W in g) according to the equation by NILSSON & NILSSON (1976):

$$\log F = -0.293 + 0.850 \log W$$

The male grebes shot weighed on an average 1288 g and the females 1031 g (Appendix 2). Assuming a mean grebe weight of 1160 g, a consumption of 205 g fish per day is estimated. Similarly, a daily food intake of 202 g fish has been derived for a mean merganser weighing 1139 g (♂♂ on an average 1267 g and ♀♀ 1010 g; Appendix 2).

To estimate the annual food consumption of the grebe and merganser populations, their daily fish intake has been multiplied by the number of bird-days. For the Cormorant and Grey Heron a daily consumption of 368 g and 248 g, respectively, was estimated on the basis of reported mean body weights from literature data (about 2312 g and 1452 g, respectively; BAUER & GLUTZ VON BLOTZHEIM, 1966; CRAMP & SIMMONS, 1977).

The thus estimated total annual fish consumption by birds in Lake Grevelingen increased from 30 metric tons in the first year after the closure to 155 tons in 1975/1976 (Table 2). Approximately over the same period the share of the grebes in the total consumption increased from 52% to 74%. As a consequence of a decline in the number of grebes in 1979/1980, the total fish consumption then decreased to less than 72 tons.

During 1981/1982 the fish consumption by birds amounted to 115 tons, or 1.1 g fresh weight (FW)$\cdot m^{-2}\cdot a^{-1}$, 46.6 (41%) and 39.2 (34%) tons of which were accounted for by the grebes and mergansers, respectively. Of the main prey species, 52 tons of small gobiid fish, 14 tons of *Crangon crangon* and 10 tons of *Clupea harengus* were consumed by the grebe and merganser populations (Table 4). In terms of numbers, these figures represent approximately 72, 18 and 1.4 million individual Gobiidae, brown shrimps and herring, respectively.

TABLE 4

The standing stocks of the main prey species as observed in September/October 1981 and the amounts and relative shares consumed by the populations of the Great Crested Grebe and Red-breasted Merganser during the subsequent winter season. The essential data about the fish stocks have been derived from regular trawling surveys. The standing stock of *Crangon crangon* is unknown.

Prey species	*Standing stock (tons FW)*		*Consumption (tons FW)*			
			Grebes	*Mergansers*	*Total*	*%*
Pomatoschistus microps	109					
Pomatoschistus minutus	26					
Gobius niger	7					
		142	28.3	23.2	51.5	36.3
Clupea harengus	36		9.9	–	9.9	27.5
Sprattus sprattus	10		3.3	–	3.3	33
Gasterosteus aculeatus	21		0.0	2.4	2.4	11.4
Atherina presbyter	32		0.3	0.1	0.4	1.3
Crangon crangon	?		2.8	11.0	13.8	?

Thus, during the winter period the grebes and mergansers consumed approximately 28 to 36% of the standing stocks of Gobiidae, *Clupea harengus* and *Sprattus sprattus* present at the arrival of the birds in September/October (Table 4), and only 11% of the population of the spiny *Gasterosteus aculeatus*. In addition, the predation of *Atherina presbyter* is remarkably low (1%).

4. DISCUSSION

Although only a small number of birds could be killed for purposes of stomach analyses, the shooting in areas where the birds were most abundant and the number of prey items identified justify the belief that the information obtained yields representative figures for the food spectrum of the grebes and mergansers foraging on Lake Grevelingen during the winter 1981/1982. Of the 2275 prey specimens identified, 76% were Gobiidae and more than 80% of the birds collected contained the remains of gobiid fish, which matches the predominance of these species in the standing stock in the lake. In addition, the prey species observed were all common to the lake and no species from outside the area were found.

Average fat contents of 18.6 ± 6.0% and 14.8 ± 5.3% were measured for the grebes and mergansers, respectively (Appendix 2). Thus, the birds shot appear to have been in good health. The grebes collected in March, however, were rather lean (on an average 10.9 ± 4.6% fat), containing significantly less fat ($p < 0.001$) than the birds from the previous months. From a sample of 750 Great Crested Grebes accidentally drowned in commercial fishing nets in Lake IJssel (The Netherlands) during the winter months of 1979/1980 and 1980/1981 (October to March), 42 selected birds (representing the range in weights) had an average fat content of 19.0% (*cf.* PIERSMA, 1984). Twelve Red-breasted Mergansers caught in the same manner, contained on an average 15% fat (M.R. VAN EERDEN, personal communication). Twenty one of the closely related Smew *Mergus albellus* shot on Lake IJssel during January to March 1977 had a fat content of 17.3 ± 4.6% (DOORNBOS, 1980).

Since the digestion rate may vary with prey type some bias might have been introduced by using long identifiable remains (otoliths, etc.) to reconstruct the size of the prey consumed. Although variations due to prey species cannot be accounted for, the close correspondence between the lengths of the intact brown shrimps found in the merganser gullets and those of the individuals reconstructed by means of the claw size (Fig. 8) indicates that size dependent variation in digestion time will not have caused a significant bias.

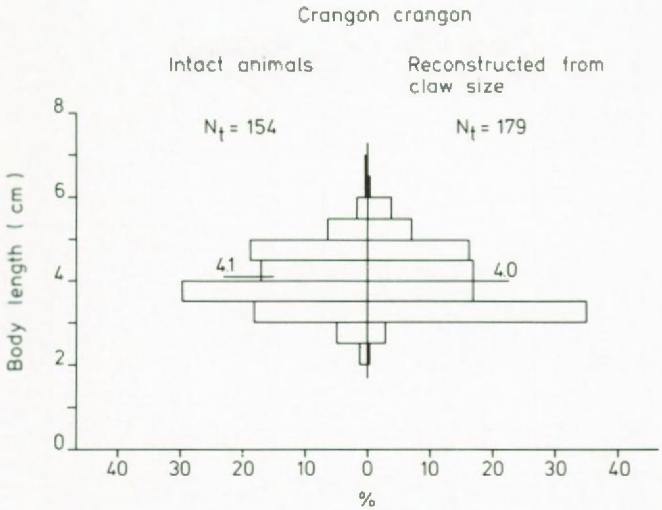


Fig. 8. Comparison of the frequency distribution of lengths of intact individuals of *Crangon crangon* found in the gullets of mergansers with that of lengths reconstructed by means of claw sizes found in the stomach contents of the birds. The average lengths are indicated by a horizontal bar.

In general, the food spectrum observed agrees well with the available literature (*e.g.* MADSEN, 1957; BAUER & GLUTZ VON BLOTZHEIM, 1966, 1969; CRAMP & SIMMONS, 1977). In brackish and marine habitats Gobiidae have been found to be the dominant food species for grebes. In addition to gobiid fish, mergansers are known to prey heavily on Gasterosteidae and crustaceans, predominantly *Crangon crangon*. Gobiidae probably represent the main food source in other years as well, as is indicated by the observed 173 otoliths of gobiid fish, 2 of *Sprattus sprattus* and 1 of *Clupea harengus* in the stomach of a deadly wounded (by Great Black-backed Gulls *Larus marinus*) grebe collected in January 1981. Moreover, a highly significant ($p < 0.01$; $n = 10$) linear correlation was found in the lake between the density of *P. microps* in one year (based on catch per unit of effort) and the number of grebe-days during the succeeding winter season (Fig. 9). On the other hand, three grebes from May 1974 contained 1 *C. harengus* and 3 *S. sprattus* (SAEIJS & BAPTIST, 1976b), although these authors neglected small items such as otoliths. At that time sprat was also more abundant than nowadays (DOORNBOS, 1982).

To assess the food requirements of the bird populations in Lake Grevelingen, WOLFF *et al.* (1976) multiplied the standard metabolic rate M, obtained from the equation of LASIEWSKI & DAWSON (1967) with

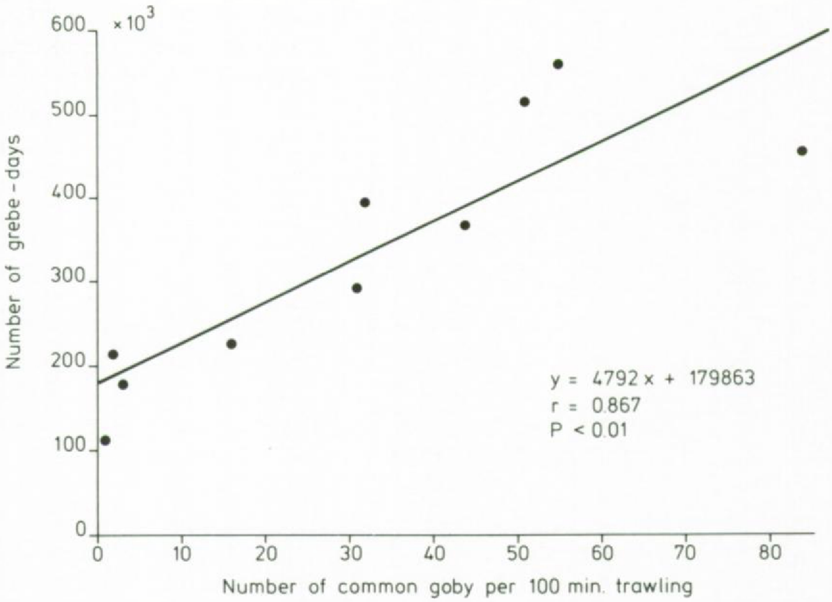


Fig. 9. Relationship between the number of common goby *Pomatoschistus microps* caught in 100-minute trawling periods over one year with the number of grebe-days in the subsequent winter season for the period 1972 to 1982. Fishing was done with a 3 metre beam trawl in an area deeper than 5 m and catches are standardized for 10 × 10 mm mesh size.

respect to nonpasserines, by 5. However, according to NILSSON & NILSSON (1976), the food intake of free-living piscivorous birds would be about 3 times the standard metabolism and 2 times the existence energy (KENDEIGH, 1970). Their equation leads to a daily intake of 17 to 18% of the body weight of a medium sized bird. Recently, KIRKWOOD (1983) has shown that only during short periods of intensely energy-demanding conditions the maximum food intake by birds and mammals may increase up to 5 times the fasting metabolic rate (= M). An average daily metabolic rate of 2.6 times M (DRENT & DAAN, 1980) results in a food consumption of approximately 0.18 g ADW (~0.9 g FW)·m^{-2}·a^{-1} by piscivorous birds in Lake Grevelingen over 1972 to 1975 (WOLFF *et al.*, 1976). In Lake Möckeln, southern Sweden, fish consumption by birds has been assessed at 0.8 g FW·m^{-2}·a^{-1} (NILSSON & NILSSON, 1976). These figures are of the same order as reported here (1.1 g FW·m^{-2}·a^{-1}) for Lake Grevelingen in 1981/1982. Only during 1975 to 1979 the fish consumption was somewhat higher, *viz.* an average of 1.3 g FW·m^{-2}·a^{-1}.

A consumption by birds of 28 to 36% of the standing stocks such as those found in Lake Grevelingen does not appear to be unrealistically high. According to AINLEY (1980), seabirds may consume about 20 to 35% of the annual prey production and since production figures for small fish such as Gobiidae only slightly exceed their maximum yearly biomass, this would agree very well with the present findings. In Oregon, in the United States of America, WIENS & SCOTT (1975) suggest that the coastal seabird populations consume as much as 22% of the pelagic fish production each year. On Foula, Shetland, one seabird community consumed 29% of the fish production within a 45 km radius around the colony (FURNESS, 1978), and in the Saldanha Bay on the west coast of South Africa, the annual cropping by birds was assessed at 24% of the biomass of round herring *Etrumeus teres*, 23% of anchovy *Engraulis capensis* and 4% of pilchard *Sardinops ocellata* (FURNESS & COOPER, 1982). Recently, FURNESS (1984) recalculated the annual fish consumption by seabirds in the North Sea, likely being close to 20% of the fish production. In October 1980, the total fish biomass in Lake Grevelingen was assessed at 632 tons FW (DOORNBOS, 1982), whereas the bird predation during the subsequent winter is estimated at 135 tons (Table 2), representing 21% of the standing stock. Considering that only part of the species is important to birds, the percentage for individual fish stocks can be somewhat higher.

With respect to prey size selection, it would be more profitable for birds to catch larger specimens because the energy content of a prey increases approximately by its length to the third power. In extensive eelgrass beds of Western Port, Australia, HOWARD & LOWE (1984) observed that the Royal Spoonbill *Platalea regia* was highly selective in cropping the larger adult females of the palaemonid shrimp *Macrobranchium intermedium*. Juveniles were hardly preyed upon. Four nestling heron species, *viz.* the Grey Heron, Purple Heron *Ardea purpurea*, Little Egret *Egretta garzetta* and Night Heron *Nycticorax nycticorax*, also showed a strong tendency to select the larger female mosquito fish *Gambusia affinis* while feeding in freshwater marshes in the Camargue, France, (BRITTON & MOSER, 1982).

An amount of 60 to 80 g fish, such as found in the stomachs of the birds in the first two months, represents about ⅓ of the daily food requirements of the birds. If that amount also represents the intake from dawn to the moment of killing, the birds would have just enough time to complete their meals before sunset. In the case of the Red-breasted Merganser this amount would not have been sufficient in the February to March period.

The significant decline in the number of gobiid remains in the stomachs of the birds during the season may be related to the density and availability of these prey species. During autumn and early winter, *Pomatoschistus minutus* and *Gobius niger* migrate into deeper water (Fig. 10; *cf.* HESTHAGEN, 1977; NASH, 1984). In December the highest densities of these fish were found below 20 m, while the shallow areas were almost completely abandoned. *P. microps* breeds in very shallow water and also migrates, although to a lesser extent than its relatives (Fig. 10; *cf.* JONES & MILLER, 1966). At the beginning of December high densities of small *P. microps* were still found in the 0 to 0.6 m zone. In the 2 to 5 m zone the density of *P. microps* amounted to four times that of *P. minutes*, actually about the same ratio as observed in intact Gobiidae collected from the gullets of the birds (*viz.* 45 (74%) *P. microps*, 14 *P. minutes* and 2 *G. niger*, respectively). According to BAUER & GLUTZ VON BLOTZHEIM (1966) and CRAMP & SIMMONS (1977), grebes forage predominantly in waters 2 to 6 m deep and mergansers in waters less than 3.5 m and occasionally up to 5.6 m. In the lake from October to January, both species were observed feeding particularly at the transitions of the shallow banks and the deeper gullies, where the water is 2

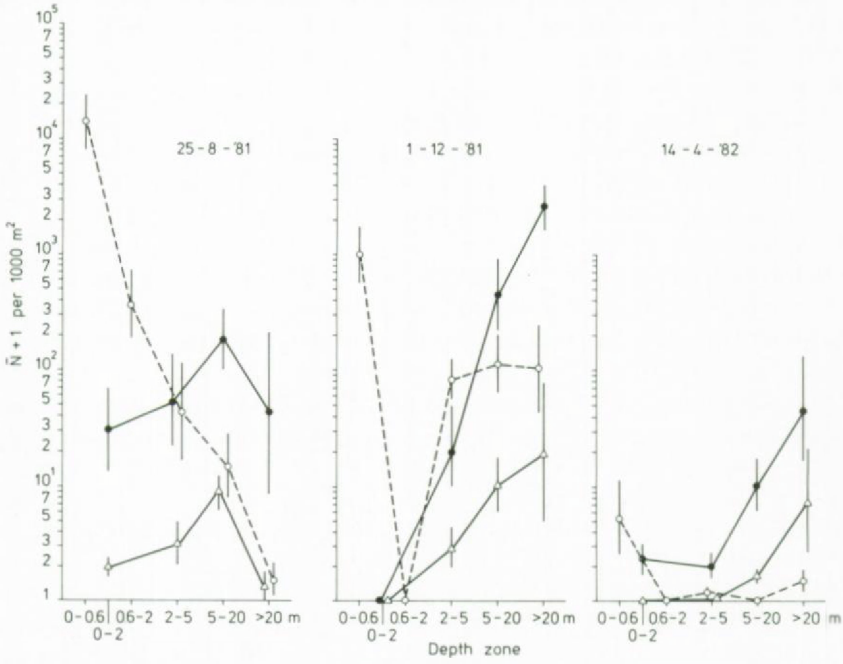


Fig. 10. Mean densities of *Pomatoschistus microps* (○ – – ○), *P. minutus* (● — ●) and *Gobius niger* (Δ — Δ) in the areas 0 to 0.6 m (18 km^2), 0.6 to 2 m (25 km^2), 2 to 5 m (27 km^2), 5 to 20 m (35 km^2) and >20 m (3 km^2) during August, December and April. The 95% confidence limits are indicated by vertical bars.

to 5 m deep. Unfortunately, it was not possible to draw a direct relation between the difference in habitat selection of the grebes and mergansers and local differences in the fish abundance.

Although grebes can dive up to 30 m (CRAMP & SIMMONS, 1977) and these birds were feeding in the most western part of the lake in waters deeper than 20 m from February to March, their stomachs hardly contained any remains of demersal fish (Fig. 6). It may be concluded that in the course of the winter season, the main prey species, the gobiid fish, grew scarce (Fig. 10). According to the estimated rate of consumption, 36% of the decline in gobiid density can be accounted for by the grebes and mergansers, whereas flatfish may add another source of mortality. The total annual consumption of gobiid fish by the latter, principally occurring from September through February, has been estimated at approximately 0.5 g $FW \cdot m^{-2} \cdot a^{-1}$ (DOORNBOS & TWISK, 1984). However, about 25% of the decline cannot be accounted for by predation by birds nor flatfish and may be due to other causes. A comparable situation was observed by COOPER *et al.* (1984) in the hypersaline Mono Lake in California, U.S.A. In this 150 km^2 lake, the predation of hundreds of thousands of foraging Eared Grebes *Podiceps nigricollis* accounted for 55 to 83% of the profound autumn decline in the brine shrimp *Artemia monica* density in 1980, but only for 8 to 27% of the decline in the *Artemia* density in 1981. Particularly in 1981, most of the *Artemia* mortality was due to other causes than predation by grebes.

5. SUMMARY

Since 1971, when the Grevelingen estuary was turned into a 108 km^2 saline lake, the number of foraging piscivorous birds has increased significantly. Up to 7000 to 10 000 Great Crested Grebes may be present on the lake, representing about half of the northwestern European breeding population. In the winter 1000 to 3000 Red-breasted Mergansers also forage here, while in summer and early autumn 500 to 800 Cormorants can be found on the lake.

From December 1981 through March 1982 the food habits of the grebes and mergansers were studied by means of stomach analyses. Total annual consumption of the two fish-eating birds was estimated at 46.6 and 39.2 tons fresh weight, respectively. Gobiidae proved to be the main food source, accounting for 60% of the total intake (by weight). In addition, the grebes consumed 9.9 tons of *Clupea harengus* and the mergansers 11.0 tons of brown shrimps *Crangon crangon*. The birds tended to select the larger specimens of Gobiidae and *C. crangon*. The estimated amount of food consumed by these two bird species represents about 28 to 36% of the standing stocks of Gobiidae, *C. harengus* and

Sprattus sprattus present at the arrival of the birds in September/October. Total annual consumption by all major piscivorous birds, including the populations of Cormorant and Grey Heron, was estimated at 115 tons ($1.1\ g\ FW \cdot m^{-2} \cdot a^{-1}$).

Over the last 10-year period the number of wintering grebes showed a positive correlation ($p < 0.01$) with the density of *Pomatoschistus microps* during the preceding (summer) season (*i.e.* the most abundant gobiid species in the lake).

6. REFERENCES

AINLEY, D.G., 1980. Birds as marine organisms: a review. CalCOFI Rep. **21:** 48-53.

BANNINK, B.A., J.H.M. VAN DER MEULEN & P.H. NIENHUIS, 1984. Lake Grevelingen: from an estuary to a saline lake. An introduction.—Neth J. Sea Res. **18:** 179-190.

BAUER, K.M. & U.N. GLUTZ VON BLOTZHEIM, 1966. Handbuch der Vögel Mitteleuropas. 1. Gaviiformes—Phoenicopteriformes. Akademische Verlagsgesellschaft, Frankfurt am Main: 94-117, 242-261, 300-322.

——, 1969. Handbuch der Vögel Mitteleuropas. 3. Anseriformes. Akademische Verlagsgesellschaft, Frankfurt am Main: 426-456.

BRITTON, R.H. & M.E. MOSER, 1982. Size specific predation by herons and its effect on the sex-ratio of natural populations of the mosquito fish *Gambusia affinis* Baird and Girard.—Oecologia **53:** 146-151.

COOPER, S.D., D.W. WINKLER & P.H. LENZ, 1984. The effect of grebe predation on a brine shrimp population.—J. Anim. Ecol. **53:** 51-64.

CRAMP, S. & K.E.L. SIMMONS, 1977. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. 1. Ostrich to ducks. Oxford University Press, Oxford: 78-89, 200-207, 302-312, 673-680.

DOORNBOS, G., 1979. Winter food habits of Smew (*Mergus albellus* L.) on lake IJssel, The Netherlands: species and size selection in relation to fish stocks.—Ardea **67:** 42-48.

——, 1980. Aantallen, verspreiding, aktiviteit, voedsel en konditie van nonnetjes (*Mergus albellus* L.) in het zuidwestelijk IJsselmeergebied, winter 1977. Rijksdienst voor de IJsselmeerpolders, Lelystad, RIJP-Report 1980-20: 1-36 (unpublished report).

——, 1981. Verwachtingen voor de ontwikkeling van de visstand in een zoute, of zoete Grevelingen tegen de achtergrond van de veranderingen die zijn opgetreden in de visfauna in de periode 1960-1980. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke and Delta Dienst RWS, Middelburg, Z 81 III 6: 1-28 (unpublished report).

——, 1982. Changes in the fish fauna of the former Grevelingen estuary, before and after the closure in 1971.—Hydrobiol. Bull. **16:** 279-283.

DOORNBOS, G. & F. TWISK, 1984. Density, growth and annual food consumption of plaice (*Pleuronectes platessa* L.) and flounder (*Platichthys flesus* (L.)) in Lake Grevelingen, The Netherlands.—Neth. J. Sea Res. **18:** 434-456.

DRENT, R.H. & S. DAAN, 1980. The prudent parent: energetic adjustments in avian breeding.—Ardea **68:** 225-252.

FURNESS, R.W., 1978. Energy requirements of seabird communities: a bioenergetics model.—J. Anim. Ecol. **47:** 39-53.

——, 1984. Seabird biomass and food consumption in the North Sea.—Mar. Pollut. Bull. **15:** 244-248.

FURNESS, R.W. & J. COOPER, 1982. Interactions between breeding seabird and pelagic fish populations in the southern Benguela region.—Mar. Ecol. Prog. Ser. **8:** 243-250.

GLAZENBURG, A.K., 1982. Interspecifieke konkurrentie als mogelijke verklaring voor aantalsfluktuaties van twee grondelsoorten in de Grevelingen (*Pomatoschistus minutus* en *P. microps*). Studentenverslag Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, D6-1982: 1-36 (unpublished report).

HESTHAGEN, I.H., 1977. Migrations, breeding, and growth in *Pomatoschistus minutus* (Pallas)(Pisces, Gobiidae) in Oslofjorden, Norway.—Sarsia **63:** 17-26.

HOWARD, R.K. & K.W. LOWE, 1984. Predation by birds as a factor influencing the demography of an intertidal shrimp.—J. exp. mar. Biol. Ecol. **74:** 35-52.

JONES, D. & P.J. MILLER, 1966. Seasonal migrations of the common goby, *Pomatoschistus microps* (Krøyer), in Morecambe Bay and elsewhere.—Hydrobiologia **27:** 515-528.

KENDEIGH, S., 1970. Energy requirements for existence in relation to size of bird.—Condor **72:** 60-65.

KIRKWOOD, J.K., 1983. A limit to metabolisable energy intake in mammals and birds.—Comp. Biochem. Physiol. **75A:** 1-3.

LASIEWSKI, R.C. & W.R. DAWSON, 1967. A re-examination of the relation between standard metabolic rate and body weight in birds.—Condor **69:** 13-23.

LEYS, H.N. & J.J.F.E. DE WILDE, 1971. Het voorkomen van de fuut *Podiceps cristatus* in Nederland.—Limosa **44:** 133-183.

MADSEN, F.J., 1957. On the food habits of some fish-eating birds in Denmark.—Dan. Rev. Game Biol. **3:** 19-83.

NASH, R.D.M., 1984. Aspects of the biology of the black goby, *Gobius niger* L., in Oslofjorden, Norway.—Sarsia **69:** 55-61.

NIENHUIS, P.H., 1978. Lake Grevelingen: a case study of ecosystem changes in a closed estuary.—Hydrobiol. Bull. **12:** 246-259.

NILSSON, S.G. & I.N. NILSSON, 1976. Numbers, food consumption, and fish predation by birds in Lake Möckeln, southern Sweden.—Ornis Scand. **7:** 61-70.

PIERSMA, T., 1984. Estimating energy reserves of Great Crested Grebes *Podiceps cristatus* on the basis of body dimensions.—Ardea **72:** 119-126.

POPOVA, O.A., 1978. The role of predaceous fish in ecosystems. In: S.D. GERKING. Ecology of freshwater fish production. John Wiley, New York: 215-249.

SAEIJS, H.L.F. & H.J.M. BAPTIST, 1976a. Vogels Grevelingenmeer. Ontwikkelingen vogelstand in een zout meer van 1971-1975. 2. Rijkswaterstaat, Deltadienst, Middelburg, Note 76-31: 1-139 (unpublished report).

——, 1976b. Het voorkomen van de fuut *Podiceps cristatus* L. op het Grevelingenmeer.—Limosa **49:** 1-8.

——, 1977. Wetland criteria and birds in a changing delta.—Biol. Conserv. **11:** 251-266.

——, 1978. Vogels de computer in.—Limosa **51:** 41-51.

WIENS, J.A. & J.M. SCOTT, 1975. Model estimation of energy flow in Oregon coastal seabird populations.—Condor **77:** 439-452.

WOLFF, W.J., 1967. Watervogeltellingen in het gehele Nederlandse Deltagebied.—Limosa **40:** 216-225.

WOLFF, W.J., A.M.M. VAN HAPEREN, A.J.J. SANDEE, H.J.M. BAPTIST & H.L.F. SAEIJS, 1976. The trophic role of birds in the Grevelingen estuary, The Netherlands, as compared to their role in the saline Lake Grevelingen. In: G. PERSOONE & E. JASPERS. Proceedings of the 10th European Symposium on Marine Biology, 2. Universa Press, Wetteren: 673-689.

APPENDIX 1

Summary of abiotic and non-food biotic items observed in the stomachs of the birds shot.

Gravel.—Small stones were found in 21 (84%) merganser stomachs with a mean weight of 0.52 ± 0.42 g per bird, up to a maximum of 1.43 g. MADSEN (1957) also observed gravel in mergansers shot in Denmark. Perhaps the stones serve in the digestion process. No stones have been found in grebes.

Feather.—All 25 grebe stomachs contained feathers, probably originating from the bird itself; the mean dry weight is 2.35 ± 1.03 g per bird (range 0.70-4.67 g). The regular intake of feathers by grebes has been reported repeatedly (*e.g.* MADSEN, 1957; BAUER & GLUTZ VON BLOTZHEIM, 1966; CRAMP & SIMMONS, 1977). However, as yet the biological meaning of this phenomenon is not quite clear.

Vegetable matter.—In several stomachs, pieces of eelgrass leaves (*Zostera marina*), *Ulva lactuca* and other seaweeds were present. In some grebe stomachs a small amount of peaty material was also observed.

Crustaceans.—The remains of several small crustaceans were found in the stomachs: 6 specimens of *Praunus flexuosus* and 1 *Idotea chelipes* in the grebes and 10 specimens of *Gammarus locusta*, 3 *P. flexuosus* and 1 *Balanus* sp. in the mergansers. These specimens are believed to have entered the digestive system as stomach content of the fish eaten by the birds, since *Pomatoschistus microps* and *P. minutus* are known to prey on these crustaceans (GLAZENBURG, 1982).

Vermes and molluscs.—The grebe and merganser stomachs contained a total of 16 and 1 pair(s) of *Nereis* jaws, respectively. In addition, 44 small jaws of an unidentified worm were traced in the mergansers. Two *Hydrobia ulvae* were also observed, as well as 1 *Mytilus edulis* of spat size and 60 opercula of an unknown gastropod in a single grebe. It is possible that all these remains originate from fish stomachs.

Parasites.—A total of 233 specimens of *Contracaecum rudolphii* were identified in the gullets and stomachs of 21 mergansers; one bird contained as much as 55 individual parasitic worms. One small specimen of *Streptocara crassicauda* was also found. In contrast to the mergansers, the grebes appeared to have very few endo-parasites. While intact individuals were not present at all, the remains of an ascarid and a spirurid worm could be traced. One bird contained the remains of four worms, believed to be *Contracaecum ovale*.

Although not parasitic to birds, 3 *Lernaeocera branchialis* found in the stomach of a single grebe are also listed here. *L. branchialis* is a parasitic copepod, living as an adult on the gills of flatfish and gadoids. The copepods must have been attached to the whiting *Merlangius merlangus*; both otoliths were found in the stomach of the particular grebe.

APPENDIX 2

Basic data of the Great Crested Grebes and Red-breasted Mergansers shot on Lake Grevelingen during December 1981 through March 1982. FW is fresh weight; the percentage of fat refers to fresh weight minus stomach content.

Collect. number	*Age/Sex*	*Collect. date*	*Bill length (mm)*	*Wing length (mm)*	*Weight (g FW)*	*Stomach cont. (g FW)*	*Liver (g FW)*	*Fat (%)*	*Fat-free dry weight (g)*
Great Crested Grebe *Podiceps cristatus*									
1	ad. ♀	03-12-81	44.2	194	959	8.6	55.3	12.6	279
2	ad. ♀	03-12-81	41.4	183	1180	46.6	48.0	29.6	307
3	ad. ♂	03-12-81	50.7	192	1222	46.6	47.1	22.5	301
4	ad. ♂	03-12-81	52.5	202	1474	40.5	69.0	18.1	379
5	juv. ♀	03-12-81	46.2	184	1047	14.6	55.0	22.3	279
6	ad. ♂	10-12-81	54.2	198	1338	18.5	69.6	20.7	340
7	ad. ♀	13-01-82	45.6	190	1122	30.7	46.1	25.3	286
8	ad. ♀	13-01-82	52.3	187	1167	16.1	47.7	20.9	281
9	ad. ♀	13-01-82	47.5	185	1234	19.6	49.6	24.0	317
10	ad. ♂	13-01-82	50.4	197	1361	22.6	63.5	22.9	361
11	ad. ♀	13-01-82	45.5	185	1071	22.8	66.1	18.9	287
12	ad. ♂	13-01-82	51.7	196	1162	11.1	55.9	15.4	339
13	juv. ♀	14-01-82	41.9	181	971	24.0	62.9	18.3	254
14	ad. ♂	10-02-82	56.8	194	1207	11.6	34.6	21.2	275
15	juv. ♂	10-02-82	54.7	201	1521	35.1	70.5	20.9	386
16	juv. ♂	10-02-82	52.2	195	1523	32.6	58.5	26.8	419
17	ad. ♀	10-02-82	48.3	182	845	7.0	33.7	17.1	238
18	juv. ♀	10-02-82	47.6	185	1022	29.6	41.0	20.5	259
19	ad. ♂	10-02-82	53.9	201	1433	28.1	48.9	22.4	350
20	juv. ♀	12-03-82	47.8	186	857	22.0	50.0	5.3	262
21	ad. ♂	18-03-82	51.4	200	1161	23.5	52.9	16.0	314
22	juv. ♀	18-03-82	45.6	186	892	12.7	47.5	12.6	248
23	ad. ♂	18-03-82	51.4	193	926	7.9	38.4	7.2	288
24	juv. ♂	18-03-82	52.6	203	1087	27.4	48.4	7.5	319
25	ad. ♂	18-03-82	54.0	196	1324	26.0	75.9	16.6	340
Red-breasted Merganser *Mergus serrator*									
1	juv. ♀	03-12-81	51.9	222	1103	24.6	44.2	16.7	275
2	ad. ♀	10-12-81	54.6	225	988	11.4	47.7	15.2	275
3	ad. ♂	10-12-81	58.9	252	1344	15.7	57.8	12.6	393
4	ad. ♂	10-12-81	57.7	246	1193	15.3	68.7	10.4	303
5	ad. ♂	10-12-81	56.9	258	1298	40.9	72.3	12.7	350
6	ad. ♀	10-12-81	51.4	232	1070	43.5	50.0	14.4	286
7	ad. ♂	13-01-82	58.5	249	1363	6.5	52.0	21.0	375
8	ad. ♀	13-01-82	55.9	231	1215	31.3	45.7	25.3	299
9	ad. ♂	13-01-82	58.3	251	1239	3.9	42.4	17.0	353
10	juv. ♀	13-01-82	52.8	217	843	8.7	43.3	6.6	197
11	ad. ♀	14-01-82	56.4	233	1267	68.8	64.6	21.5	312
12	ad. ♂	14-01-82	58.9	246	1289	36.4	53.9	14.8	291
13	ad. ♀	10-02-82	53.0	226	972	36.7	50.8	10.8	286
14	juv. ♀	10-02-82	54.4	225	1025	6.2	42.7	18.9	274
15	ad. ♀	10-02-82	56.5	235	1026	19.8	42.0	16.5	289
16	ad. ♂	10-02-82	57.0	238	1130	12.8	43.0	16.5	319
17	ad. ♂	10-02-82	62.9	257	1305	24.2	52.0	13.9	368
18	ad. ♀	10-02-82	53.4	228	1112	30.3	47.8	16.5	292
19	ad. ♀	12-03-82	55.7	233	951	18.6	35.8	12.7	268
20	ad. ♀	12-03-82	52.4	227	864	5.8	52.0	13.4	252
21	ad. ♀	12-03-82	51.9	232	945	26.7	57.0	11.3	272
22	ad. ♂	12-03-82	58.7	255	1119	6.3	47.1	13.7	323
23	ad. ♀	12-03-82	50.5	230	763	12.5	34.3	3.2	229
24	ad. ♂	18-03-82	62.6	248	1308	26.4	48.1	8.5	374
25	ad. ♂	18-03-82	57.1	255	1350	1.9	38.1	26.6	352

CHAPTER 7
HOOFDSTUK

DE VISFAUNA VAN HET GREVELINGENMEER (ZW NEDERLAND):

de rol van vissen in de voedselketen
van een zoutwatermeer, circa tien jaar na
de afsluiting van het vroegere estuarium

door

GEERDINUS DOORNBOS

SAMENVATTING

Inleiding

In de nacht van 31 januari op 1 februari 1953 werd het zuidwestelijk deel van Nederland getroffen door een uitzonderlijk zware stormvloed. Ongeveer 1800 mensen verdronken en tienduizenden hektaren kultuurgrond kwamen onder water te staan. Om een herhaling van een dergelijke watersnoodramp te voorkomen besloot de regering om alle estuaria in ZW Nederland, met uitzondering van de Westerschelde, de belangrijkste zeeweg naar de haven van Antwerpen, af te sluiten (Duursma *et al.*, 1982; Bannink *et al.*, 1984).

Om waterbouwkundige redenen werd de Grevelingen eerst aan de oostzijde afgesloten door de aanleg van de Grevelingendam in 1964. Met het gereedkomen van de Brouwersdam in 1971 werd de invloed van de Noordzee buitengesloten en werd het zoute Grevelingenmeer een feit (Bannink *et al.*, 1984).

Door de aanleg van de Brouwerssluis (capaciteit 100 - 140 $m^3.s^{-1}$) werd in 1978 de verbinding met de Noordzee gedeeltelijk hersteld, terwijl in 1983 een hevel met een capaciteit van ca. 100 $m^3.s^{-1}$ (Flakkeese spuisluis) gereed kwam in de Grevelingendam. Door met beide sluizen te manipuleren kan er in het gehele Grevelingenmeer een kunstmatig stromingspatroon worden opgewekt.

In het meer daalde de chloride-koncentratie geleidelijk van 17 $^0/oo$ Cl^- in 1971 tot minder dan 13 $^0/oo$ Cl^- in 1978. Vanaf 1979 wordt de chloriniteit min of meer konstant gehouden op ca. 16 $^0/oo$ Cl^- door gedurende de winter (hoofdzakelijk van half oktober tot begin maart) meerwater uit te wisselen tegen Noordzee-water. Alleen in 1979 stond het doorlaatwerk in de Brouwersdam het gehele jaar open (Bannink *et al.*, 1984).

In 1957 werd het Delta Instituut voor Hydrobiologisch Onderzoek, als onderdeel van de Koninklijke Nederlandse Akademie van Wetenschappen, opgericht. De taak van het Delta Instituut was (is) het bestuderen van de eventuele veranderingen in de flora en fauna als gevolg van de afsluiting van de verschillende riviermondingen en zeearmen in het Deltagebied. Sinds ca. 1970 heeft het instituut zich geleidelijk meer toegelegd op het onderzoek naar het funktioneren van oecosystemen in "stress" situaties, bijvoorbeeld als gevolg van grote waterbouwkundige werken (Duursma & Nieuwenhuize, 1985).

In 1972 startte de werkgroep "Koolstofkringloop in de Grevelingen" van het Delta Instituut een oecosysteem-studie, die het kwantificeren van het organisch materiaal door de voedselketen in het zich pas ontwikkelende zoutwatermeer tot doel had (Nienhuis, 1978a, 1978b). Door de vaste staf van de werkgroep konden echter niet alle noodzakelijk geachte facetten van het onderzoek worden uitgevoerd (Bannink *et al.*, 1984).

In maart 1979 gaf de Directeur-Generaal van Rijkswaterstaat machtiging tot het doen verrichten van een aanvullende oecologische studie in het Grevelingenmeer. Hoewel gefinancierd door Rijkswaterstaat, werd de feitelijke uitvoering alsook de uiteindelijke wetenschappelijke verantwoordelijkheid van het ZOWEC (ZOut Water ECologie)-projekt uitbesteed aan het Delta Instituut, dat tevens de initiatieven voor dit projekt had ontplooid. Het ZOWEC-projekt omvatte vijf onderdelen, die volledig in het onderzoeksprogramma van de werkgroep "Koolstofkringloop in de Grevelingen" pasten:

1. Mineralisatie van organisch materiaal in het water (Goossens *et al.*, 1983).
2. Mineralisatie van organisch materiaal op en in de bodem (Lindeboom & de Klerk - van der Driessche, 1983).
3. Kwantitatief visonderzoek (Doornbos *et al.*, 1986).
4. Bodem-water uitwisseling (Kelderman, 1983).
5. Scheiding en kwantificering van seston (van Ierland & Peperzak, 1982).

Deel 3 van het projekt had tot doel het kwantificeren van de rol van de vissen in de voedselketen van het meer op basis van aantallen, groei (produktie), prooiselektie en jaarlijkse voedselkonsumptie, alsook hun rol bij de overdracht ven energie van de lagere trophische niveaux (*e.g.* opgeslagen in zoöplankton en zoöbenthos) naar de hogere (*e.g.* beschikbaar voor visetende vogels). Het eigenlijke onderzoek heeft zich gericht op: 1) de voedselsamenstelling en voedselopname van de belangrijkste vissoorten in het meer en 2) de predatie van vissen door hun belangrijkste predatoren.

Reeds sinds 1960 worden de verschillende Deltawateren bemonsterd met een 3 m boomkor teneinde eventuele veranderingen in de visfauna, tengevolge van de uitvoering van het Delta Plan, op te kunnen sporen (*cf*. Vaas, 1970, 1979). Daardoor konden eveneens de meest opvallende effekten van de waterstaatkundige werken op de oorspronkelijke visfauna van de Grevelingen worden bestudeerd.

In dit proefschrift zijn de belangrijkste resultaten van het ZOWEC-vissenprojekt als afzonderlijke hoofdstukken opgenomen. Een gedeelte hiervan is reeds eerder verschenen in wetenschappelijke tijdschriften.

Resultaten, aangevuld met recente ontwikkelingen

In Hoofdstuk 2 wordt een overzicht gegeven betreffende de veranderingen die in de Grevelingen gedurende 1960 - 1980 zijn opgetreden als gevolg van de in die periode uitgevoerde waterbouwkundige werken. Na de afsluiting in 1971 daalde het aantal met de 3 m boomkor gevangen vissoorten sterk. Ofwel een aantal vissoorten was geheel uit het meer verdwenen, of hun aantallen waren te laag geworden om nog te worden opgemerkt tijdens de bemonsteringen. Het aantal vissoorten nam weer toe na het openen van de Brouwerssluis in 1979.

In het Grevelingenmeer zijn gedurende 1979 - 1982 in totaal 59 vissoorten, behorende tot 31 families, waargenomen (Appendix 1). Dit is betrekkelijk weinig in vergelijking met de ca. 100 vissoorten in de Waddenzee (Witte & Zijlstra, 1978) en in de Oosterschelde (Doornbos *et al*., 1981), of met de 134 soorten die in het Nederlandse kustgebied zijn waargenomen (Nijssen & de Groot, 1980). Het aantal vissoorten in de Nederlandse estuaria blijkt trouwens goed overeen te komen met het aantal waargenomen soorten in soortgelijke gebieden in Groot-Brittannië, bijvoorbeeld 97 soorten in het Severn estuarium (Claridge *et al*., 1986) en 98 soorten in het Theems estuarium (Andrews, 1984). Het daarbij vergeleken geringe aantal soorten in het Grevelingenmeer lijkt een direkt gevolg te zijn van de afsluiting, waardoor vele dwaalgasten niet meer worden waargenomen.

Het totale aantal en de biomassa van *Pomatoschistus microps*, zoals geschat in Hoofdstuk 2 op basis van de boomkorvangsten in 1980 (Tabel II), is ongetwijfeld een onderschatting, aangezien in latere onderzoekingen deze soort vooral erg talrijk bleek te zijn in het in 1980 niet bemonsterde litorale deel van het meer (zie ook Hoofdstuk 5).

De jaarlijkse aalvangsten *Anguilla anguilla* door de beroepsvissers blijken nog steeds licht te stijgen, van gemiddeld 69 ton gedurende 1972 - 1977 tot ca. 85 ton (*i.e.* 0.8 g versgewicht (VG).m^{-2}) gedurende 1979 - 1982. Dit laatste cijfer moet als een minimale schatting van de jaarlijkse aalproduktie worden beschouwd, aangezien sinds 1979 in de herfst een deel van de populatie door de Brouwerssluis kan ontsnappen, terwijl de toenemende aantallen aalscholvers *Phalacrocorax carbo* ook hun aandeel zullen opeisen.

Volgens H.W. de Nie (1987, mondelinge mededeling) konsumeert aal gedurende het groeiseizoen dagelijks gemiddeld 2% (range 0,8 - 3%) van zijn eigen lichaamsgewicht. Uitgaande van een minimale jaarlijkse produktie van 85 ton VG, een P/B ratio van 0,5 (Doornbos, 1982, 1985) en een groeiseizoen van 183 dagen (ruwweg van half april tot half oktober), kan de jaarlijkse konsumptie door de aalpopulatie in het Grevelingenmeer worden geschat op tenminste 622 ton VG ($\sim$ 1,0 g asvrij-drooggewicht (ADG).m^{-2}). Dit getal ligt in dezelfde orde van grootte als de konsumptie die voor de botpopulatie in 1980 werd bepaald (*cf.* Doornbos & Twisk, 1984).

Wanneer de hogere opbrengst als een indikatie voor een toename van de aalbiomassa in het meer mag worden beschouwd, dan zou dit kunnen wijzen op verbeterde voedselomstandigheden voor de aal. Mogelijk is dit effekt toe te schrijven aan de afname van de schol- en botbestanden (zie ook Hoofdstuk 3), waardoor meer voedsel voor de aal beschikbaar kwam. Het aanbod aan macrozoöbenthos is gedurende die tijd hoog ($\sim$ 30 g ADG.m^{-2}) en redelijk stabiel geweest (Lambeck, 1985). Over eventuele veranderingen in de vangefficiëntie bij de beroepsvisserij op aal is niets bekend, maar deze zullen vermoedelijk niet groot zijn. In aalmagen zijn resten van wormen, crustaceeën (vooral garnaal *Crangon crangon* en strandkrab *Carcinus maenas*), mollusken (hoofdzakelijk broedjes van tweekleppigen), grondels en sprotten *Sprattus sprattus* (alleen gegeten door de grotere aal) aangetroffen. Helaas ontbraken tijd en middelen om de prooiselektie, groei en voedselkonsumptie van deze soort meer in detail te bestuderen.

Bij vergelijking van de lengte-samenstelling van de gevangen aal in de standaard boomkor (6 x 6 mm maaswijdte) en in een pelagische trawl (35 m^2 netopening en 8,5 x 8,5 mm maaswijdte), bleek de boomkor duidelijk kleinere aal te vangen (Fig. 1). Het is bovendien opmerkelijk dat in 1981 en 1982 aal kleiner dan respektievelijk ca. 40 cm en 30 cm hoofdzakelijk met de boomkor werd gevangen, terwijl de grotere exemplaren juist met de pelagische trawl werden gevangen. Een dergelijk verschil kan nauwelijks uit het

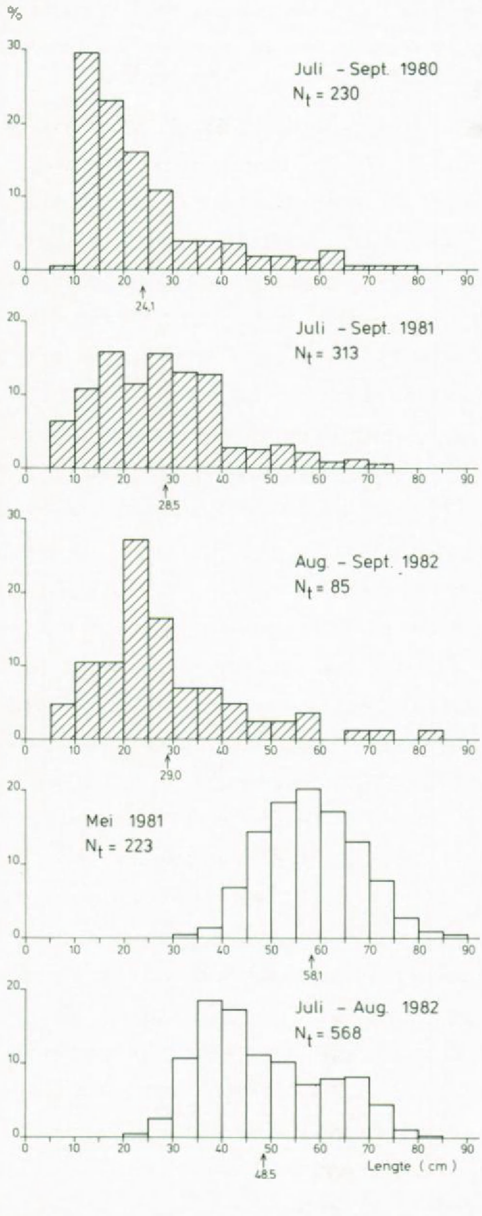


Fig. 1. Lengte-frequentieverdeling van aal in het Grevelingenmeer gedurende 1980 - 1982. Er is onderscheid gemaakt in aal gevangen met een boomkor (gearceerd) en gevangen met een pelagische trawl (blank). Door middel van een pijl is voor elke groep de gemiddelde lengte aangegeven.

verschil in maaswijdte worden verklaard en dit lijkt er op te wijzen, dat 's zomers tenminste een deel van de grotere aal zich overwegend pelagisch ophoudt.

Sinds 1979 is *Atherina boyeri* niet meer waargenomen. Vermoedelijk geeft de kleine koornaarvis de voorkeur aan wat lagere zoutgehaltes (*cf.* Wheeler, 1978), aangezien deze soort nog wel aanwezig was in het brakke Veerse Meer (P. de Koeijer, mondelinge mededeling). Bamber & Henderson (1985) hebben echter onlangs op basis van een meervoudige variantie-analyse, uitgevoerd op een serie karakteristieke morphometrische en meristische eigenschappen van een aantal koornaarvispopulaties rond de Britse Eilanden, aangetoond, dat *A. presbyter* en *A. boyeri* in feite de beide uitersten vertegenwoordigen in de verdeling van een kontinue morphologische reeks en zij konkluderen daarom dat het beter is om beide vormen als behorende tot één en dezelfde soort te beschouwen, *i.e. Atherina boyeri*. Dit is mede gebaseerd op het feit, dat de morphologische kenmerken van *A. boyeri* sterk kunnen variëren als gevolg van temperatuur- en zoutinvloeden gedurende de embryonale ontwikkeling. Vooral in geïsoleerde populaties, en daarom met name in afgesloten wateren, zouden verschillende morphologische kenmerken tengevolge van een specifieke lokale selektiedruk of een toevallige verschuiving in een aantal erfelijke eigenschappen (random genetic drift), zich gedurende een bepaalde tijd in stand kunnen houden. Het lijkt aannemelijk dat dit ook van toepassing is op de populatie van de koornaarvissen in het Grevelingenmeer.

In Hoofdstuk 3 wordt de status van de dominante platvissoorten in het meer, te weten schol en bot, beschreven aan de hand van aantallen, populatie-opbouw, groei, menu en jaarlijkse voedselkonsumptie. Na de afsluiting in 1971 slaagden de opgesloten platvispopulaties er niet in zich met succes voort te planten, hetgeen tot een vergrijzing van de beide populaties leidde. Op basis van de afname van het aantal schol gevangen per 100 minuten korren, werd een gemiddelde jaarlijkse sterfte van 33% berekend. Dankzij de uitstekende groei nam de biomassa, ondanks de teruglopende aantallen, in de eerste jaren na de afsluiting nog toe, tot een maximum van ca. 1100 ton (10,2 g VG.m^{-2}) in 1974 (Doornbos, 1985).

Gedurende 1979 - 1981 werden de beide platvispopulaties gedomineerd door de jaarklas 1979. Hoogstwaarschijnlijk zijn deze vissen als larve het meer binnengekomen door de Brouwerssluis, die in 1979 het gehele jaar open stond. In 1982 begon de invloed van deze jaarklas echter duidelijk te verminderen (zie ook de Fign 2 en 3). Ook na de verbeterde intrek in 1979 bleef het aantal aanwezige schollen ver beneden het geschatte aantal in het jaar van afsluiting, waarvan moet worden aangenomen dat het representatief is voor de dichtheid in het vroegere estuarium.

Aangezien de relatief grote vissen (vergeleken met estuariene populaties) uitstekend groeiden, was de gekombineerde konsumptie door de schol- en botpopulatie nog aanzienlijk, respektievelijk 2,8 g ADG.m^{-2} in 1980 en 1,9 g.m^{-2} in 1981. Gedurende beide jaren was de konsumptie door schol alleen bijna 1,6 g ADG.m^{-2}. De biomassa van schol werd in 1971 op ca. 8,3 g VG.m^{-2} geschat (Doornbos, 1985), hetgeen 5,5 keer meer is dan de gemiddelde biomassa over 1980 en 1981 (*i.e.* 1,5 g VG.m^{-2}). Uitgaande van deze verhouding en eenzelfde voedselkonversie gedurende beide periodes, kan voor de scholpopulatie van 1971 een voedselkonsumptie van ruwweg 9 g ADG.m^{-2} worden berekend. Aangezien de Grevelingen in mei 1971 werd afgesloten vertegenwoordigt die 9 g ADG.m^{-2} min of meer de jaarkonsumptie in het vroegere estuarium. Voor de droogvallende platen op het Balgzand (Waddenzee) berekenden Kuipers (1977) en de Vlas (1979) een jaarlijkse voedselkonsumptie door jonge schol van ca. 5 - 6 g ADG.m^{-2}. Voor het intergetijdengebied van het vroegere Grevelingen estuarium schatten Wolff *et al.* (1981) de voedselopname door uitsluitend II-groep schol op 1,5 g ADG.m^{-2} gedurende de periode maart tot mei 1971. Hieruit kan een jaarlijkse konsumptie van ruwweg 4 g ADG.m^{-2} worden afgeleid. Een jaarlijkse konsumptie van 9 g ADG.m^{-2} voor zowel de droogvallende platen als de diepere geulen, zoals voor de "estuariene situatie" van 1971 is berekend, lijkt daarom zeer aannemelijk.

Borstelwormen (Polychaeta) bleken het meest te worden gegeten, gemiddeld 56% (gewichtsaandeel) voor schol en 45% voor bot. Hierbij moet er op worden gewezen, dat er duidelijke verschillen in het menu werden gevonden tussen 1980 en 1981.

Sinds 1980 staat de Brouwerssluis hoofdzakelijk open van ongeveer half oktober tot 1 maart (Tabel 1). Dit spuiregiem biedt oudere schol en bot in principe de mogelijkheid om in de herfst naar de Noordzee weg te trekken (Steinmetz & Slothouwer, 1979; Doornbos, 1981; Klein Breteler, 1986; *cf.* Fign 2a en 2b; *cf.* Fign 3a en 3b). Aangezien anderzijds de grootste koncentratie van schollarven in maart en april en die van de bot pas in april op de kust verschijnen (Rijnsdorp *et al.*, 1985; van der Veer,

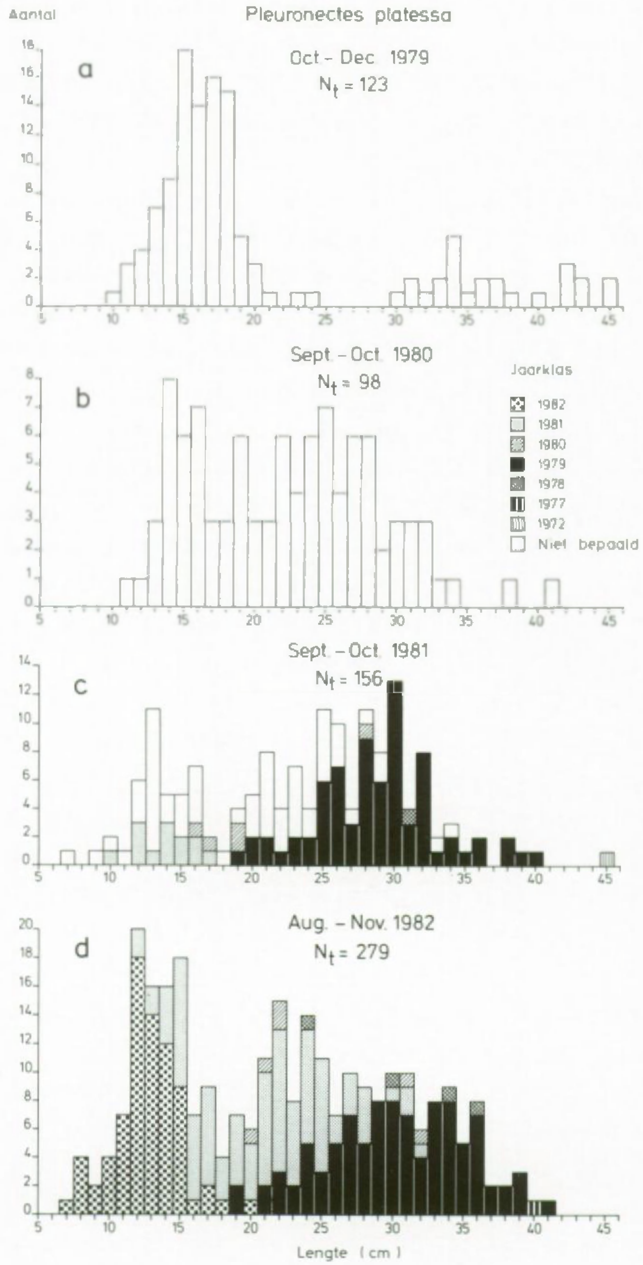


Fig. 2. Lengte-frequentieverdeling van schol in: a) 1979, b) 1980, c) 1981 en d) 1982. Van de vissen uit 1981 (een deel) en 1982 is tevens de leeftijd bepaald.

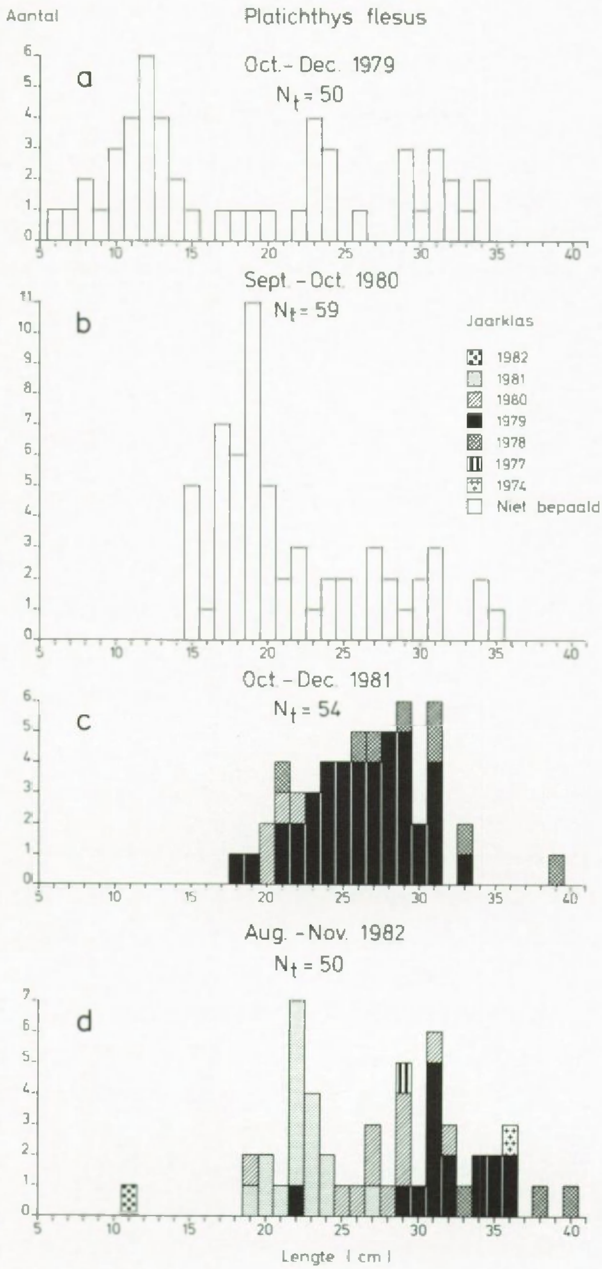


Fig. 3. Lengte-frequentieverdeling van bot in: a) 1979, b) 1980, c) 1981 en d) 1982. Van de vissen uit 1981 en 1982 is tevens de leeftijd bepaald.

1985), verhindert dit sluisbeheer tevens dat laat arriverende larven nog naar binnen kunnen trekken.

Tabel 1. Aantalsverloop schol in het Grevelingenmeer gedurende 1979 - 1985 (dus na het in gebruik nemen van de Brouwerssluis in december 1978), gebaseerd op de bestandsopnames omstreeks half september van ieder jaar, en het geschatte aantal schollarven dat ieder voorjaar naar binnen is getrokken (voor berekeningswijze zie Doornbos & Twisk, 1984). Naar eigen gegevens (1979 - 1982), aangevuld met die van Klein Breteler (1986).

Jaar	Brouwerssluis open	0-groep (x 10^6)	≥1 jaar (x 10^6)	Totaal (x 10^6)	Intrek aan larven (x 10^6)
1979	4 dec. '78 –	1,5	0,5	2,0	10,3
1980	– 1 maart '80	0,1	1,2	1,3	0,8
1981	half okt. '80 - 1 april '81	0,2	0,7	0,9	1,4
1982	half okt. '81 - 11 maart '82	0,2	0,4	0,6	1,5
1983	half okt. '82 - 1 maart '83	0,1	0,2	0,3	0,8
1984	half okt. '83 - 1 maart '84	0,1	0,2	0,3	0,8
1985	half okt. '84 - 22 maart '85	0,7	0,2	0,9	4,8

Zoals kon worden verwacht, leidde het huidige sluisbeheer na het lichte herstel in 1979 tot een kontinue afname van de scholpopulatie (Klein Breteler, 1986; Tabel 1). In tegenstelling tot de voorgaande jaren stond de Brouwerssluis in het voorjaar van 1985 echter open tot 22 maart. Dit resulteerde in een relatief goede intrek van schollarven en de afname van het aantal schol kwam tot staan. Het inlaten van Noordzee-water via de Brouwerssluis in kombinatie met het spuien van overtollig meerwater via de pas gereedgekomen Flakkeese spuisluis in de Grevelingendam heeft in het voorjaar van 1985 blijkbaar geleid tot een relatief hogere retentie van schollarven die afkomstig zijn uit het kustwater (Tabel 1). Deze gegevens onderstrepen nogmaals, dat, om de intrek te verbeteren en een grotere scholpopulatie in het meer te kunnen opbouwen, het doorlaatwerk in de Brouwersdam in het voorjaar tenminste tot en met april open moet staan en bij voorkeur in kombinatie met de Flakkeese spuisluis (*cf.* Doornbos, 1985).

De grootte van de intrek hangt daarnaast natuurlijk ook van de sterkte van de desbetreffende jaarklas in de Noordzee af. Bij schol is het verschil tussen zwakke en sterke jaarklassen globaal een faktor tien (*cf.* Zijlstra *et al.*, 1982; Anonymus, 1982, 1984, 1985) en vergelijkbare verschillen in de jaarlijkse larvenintrek zijn ook bij het Grevelingenmeer te verwachten.

Bij een kontinuering van het huidige sluisbeheer (hoofdzakelijk open tot 1 maart en incidenteel tot 1 april) mag dan ook worden verwacht, dat het totale aantal schol in het Grevelingenmeer in de nabije toekomst rond de 0,5 miljoen exemplaren zal schommelen (Tabel 1).

Voor bot is de situatie nog ongunstiger, omdat de pelagische larven voor het merendeel pas in april in de estuaria verschijnen (van der Veer, 1985). Als gevolg daarvan werd er in het meer gedurende 1980 - 1982 geen 0-groep bot waargenomen (Fig. 3). In die tijd nam de populatie af van 0,7 miljoen botten in 1980 tot ca. 0,1 miljoen stuks in 1982. Alleen als de doorlaatsluis tot in mei open zou staan, zou de botpopulatie zich enigszins kunnen herstellen. Onder de huidige omstandigheden valt echter slechts te verwachten, dat de aantallen nog verder zullen afnemen. Aangezien er, behalve aal, weinig vissen in het meer zijn die op macrozoöbenthos prederen, lijkt het oecologisch verantwoord om zoveel mogelijk schol- en botlarven het meer binnen te laten trekken en zo een groter platvisbestand op te bouwen.

In Hoofdstuk 4 wordt speciale aandacht besteed aan de spektakulaire groei van de 0-groep schol in het Grevelingenmeer. De hier bereikte lengten en gewichten gedurende het eerste groeiseizoen overtreffen alle bekende literatuur-waarden voor natuurlijke wateren. De snelle groei is goed te illustreren door een vergelijking van de bereikte gemiddelde lengten in het meer in 1981 en 1982 met die van de nabij gelegen Oosterschelde (Tabel 2). Alleen bij schol, die werd gekweekt in experimentele vijvers waar een deel van het warme koelwater van de kerncentrale van Hunterston (Schotland) doorheen werd geleid, werden vergelijkbare of zelfs nog wat hogere groeisnelheden bereikt (Bardach *et al.*, 1972).

Tabel 2. Vergelijking van de gemiddelde lengte ($\bar{L}$ in cm ± s.d.) van 0-groep schol aan het einde van hun eerste groeiseizoen uit het Grevelingenmeer met die van even oude en tot dezelfde jaarklas behorende vissen uit de Oosterschelde. De gegevens van de Oosterschelde zijn afkomstig van A.D. Rijnsdorp (mondelinge mededeling).

Jaar	Grevelingen	Oosterschelde
1981	13,0 ± 2,0	9,4 ± 1,5
1982	14,5 ± 3,4	8,7 ± 2,0

Aangezien de lengte-toename van de jonge schol in het meer goed kon worden beschreven met een door Fonds (1979) ontwikkelde empirische formule, gebaseerd op kweek-experimenten bij verschillende temperaturen, werd gekonkludeerd dat de waargenomen snelle groei hoofdzakelijk een gevolg moet zijn van de relatief hoge watertemperaturen in het meer. Er werden geen aanwijzingen gevonden voor het bestaan van dichtheids-afhankelijke effekten of dat de voedselomstandigheden een beperkende faktor zouden kunnen vormen.

De groeisnelheden voor bot (jaarklas 1979) waren in het Grevelingenmeer ook uitzonderlijk hoog (Tabel 3).

In Hoofdstuk 5 worden de dichtheid, de groei, het menu en de voedselkonsumptie van de belangrijkste Gobiidae, zijnde de brakwatergrondel *Pomatoschistus microps*, het dikkopje *P. minutus* en in mindere mate de zwarte grondel *Gobius niger*, beschreven. De grondels blijken in de voedselketen van het Grevelingenmeer een sleutelpositie in te nemen. In kwantitatief opzicht vormen de grondels bij het doorgeven van energie van de lagere trophische niveaux naar de hogere ongetwijfeld de belangrijkste groep vissen.

Tabel 3. Gemiddelde lengte (L in cm) van botten aan het einde van hun eerste (L_1), tweede (L_2), derde (L_3) en vierde (L_4) groeiseizoen in verschillende Europeese wateren.

Gebied	L_1	L_2	L_3	L_4	Bron
Grevelingenmeer	11,2	∿18,5	26,3	31,5	Dit onderzoek
Rivier de Frome	8,9	15,1	22,5	30,4	Beaumont & Mann, 1984
Taymar estuarium	7,6	14,7	20,5	28,9	Hartley, 1940
Ythan estuarium	7,4	15,0	21,9	27,2	Summers, 1979
Oostzee	-	11,5	16,0	19,5	Kandler, 1932[1)]
Oostzee	4,4	11,1	16,3	20,1	Cieglewicz *et al.*, 1969[1)]

1) *Vide* Beaumont & Mann (1984)

Vergeleken met andere gebieden zijn de in het Grevelingenmeer gevonden dichtheden hoog, terwijl de groei vrij goed is te noemen. Als gevolg hiervan is hun jaarlijkse voedselkonsumptie, overwegend bestaande uit copepoden (ruwweg een gewichtsaandeel van 90%) en andere kleine epibenthische crustaceeën, aanzienlijk. Voor beide *Pomatoschistus*-soorten tezamen werd een maximale konsumptie van 3,5 g ADG.$m^{-2}.j^{-1}$ berekend. De grondels hebben op hun beurt echter ook te lijden van een hoge mortaliteit. Zij bleken te worden gegeten door verscheidene predatoren, waaronder meerdere platvissoorten (schol, bot, schar *Limanda limanda*, tarbot *Scophthalmus maximus* en griet *S. rhombus*), aal, zeedonderpad *Myoxocephalus scorpius*, haring *Clupea harengus*, puitaal *Zoarces viviparus* en vogels. In 1981/1982 bestond het voedsel van de doortrekkende en overwinterende populaties van de fuut *Podi-*

ceps cristatus en de middelste zaagbek *Mergus serrator* bijvoorbeeld voor 60% (gewichtsaandeel) uit grondels. Een schatting leert, dat ca. 60% van de in de nazomer aan grondels aanwezige gewichtshoeveelheid door vogels en platvissen wordt weggegeten (zie ook Hoofdstuk 6).

Het is op het ogenblik echter nog niet geheel duidelijk waardoor de waargenomen jaarlijkse fluktuaties in de dichtheid van de grondels worden veroorzaakt. De achteruitgang van de *P. microps* populatie in 1979 kan vermoedelijk worden toegeschreven aan de strenge winter van dat jaar. Het duurde daarna bijna twee jaar voordat de populatie zich had hersteld.

In Hoofdstuk 6 wordt de rol van de visetende vogels in de voedselketen beschreven in termen van aantallen, prooikeuze en jaarlijkse voedselkonsumptie. Na de afsluiting in 1971 namen de futen *Podiceps cristatus*, middelste zaagbekken *Mergus serrator* en aalscholvers *Phalacrocorax carbo*, die op het meer gedurende een deel van het jaar komen pleisteren en foerageren, enorm in aantal toe.

Het aantal overwinterende futen schijnt, na een inzinking gedurende de periode 1979 - 1983, weer terug te keren op het oorspronkelijke niveau. Dit kan zowel worden afgeleid uit de resultaten van de vogeltellingen van de afgelopen jaren (Meininger *et al.*, 1985; Fig. 4a) alsook uit het aantal berekende fuut-dagen dat jaarlijks op het meer wordt doorgebracht (Fig. 5a). Ook het aantal overwinterende zaagbekken neemt nog steeds toe (Fig. 4b en Fig. 5b) en tegenwoordig zijn winter-maxima van 2400 à 3800 vogels geen zeldzaamheid meer. Dit is twee à drie keer meer dan in de periode van voor 1978. De grootste toename valt echter zonder twijfel bij de aalscholver waar te nemen. Vanaf 1982 liggen de herfst-pieken rond de 2000 individuen (Fig. 4c), terwijl het jaarlijks op het meer doorgebrachte aantal aalscholver-dagen, vergeleken met de periode van 1972 - 1979, ruwweg met een faktor vier is toegenomen (Fig. 5c).

Uitgaande van de recente aantalsontwikkelingen bij deze drie talrijkste visetende vogelsoorten lijkt de verwachting gerechtvaardigd, dat de prooidichtheid nog geen beperkende faktor vormt. Over de bestandsontwikkelingen van de kleine prooivissen in het meer na 1982 is echter niets bekend. Wanneer wij aannemen dat het gewichtsaandeel van grondels in de menu's van de futen en zaagbekken hetzelfde (*i.e.* 60%) is gebleven (*cf.* Hoofdstuk 6), zou dat betekenen dat de beide vogelpopulaties in 1984/1985 ca. 107 ton grondels zouden hebben gekonsumeerd (hetgeen in 1981/1982 51,5

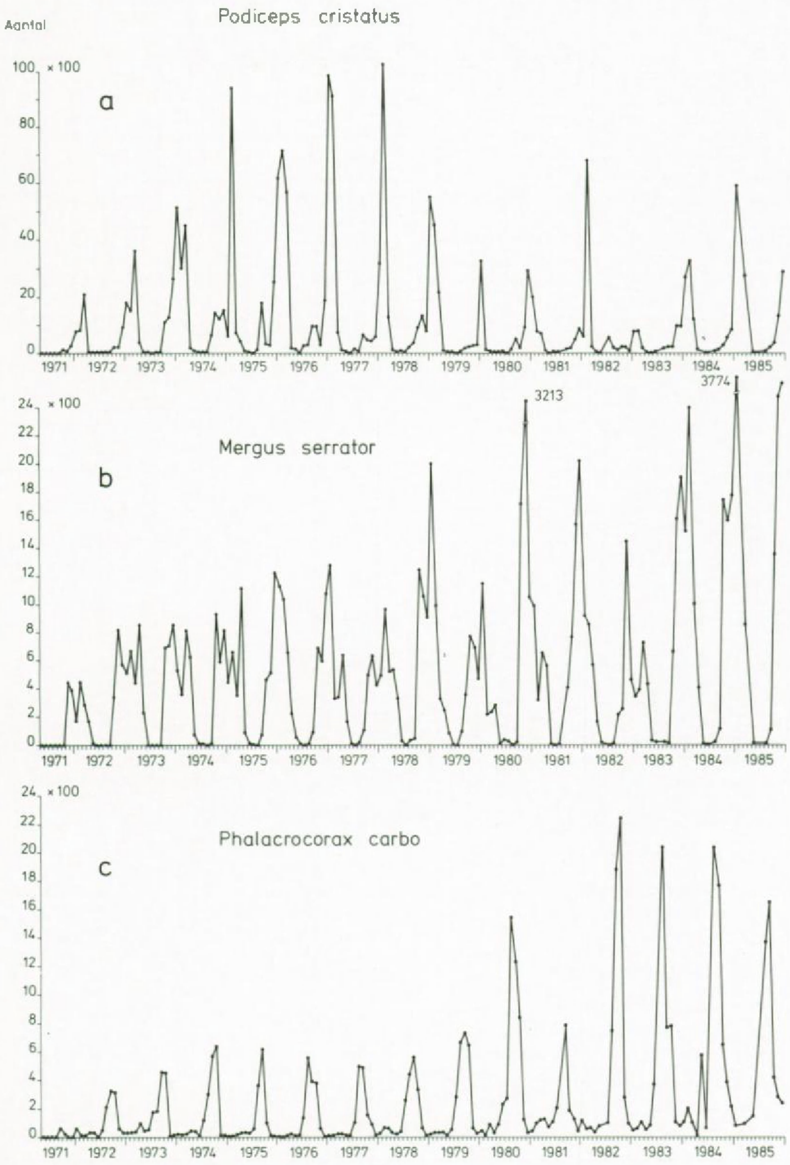


Fig. 4. Aantalsverloop, op basis van maand-maxima, van: a) fuut *Podiceps cristatus*, b) middelste zaagbek *Mergus serrator* en c) aalscholver *Phalacrocorax carbo*. De gegevens zijn afkomstig van de door het Staatsbosbeheer uitgevoerde vogeltellingen (zie ook Meininger *et al.*, 1984, 1985).

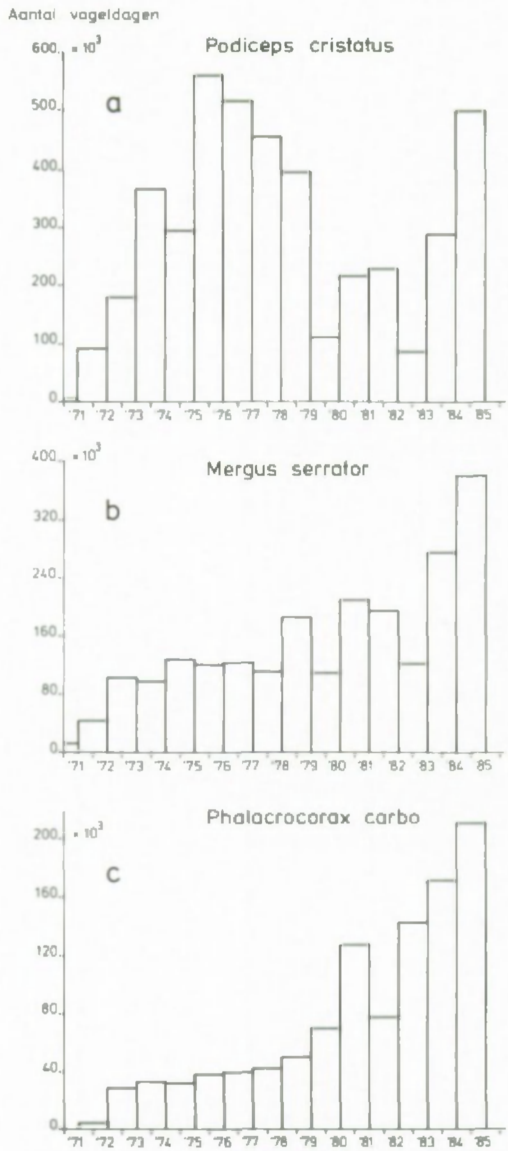


Fig. 5. Ontwikkeling van het aantal vogeldagen van: a) fuut *Podiceps cristatus*, b) middelste zaagbek *Mergus serrator* en c) aalscholver *Phalacrocorax carbo*, in het Grevelingenmeer gedurende 1971 - 1985. Het aantal vogeldagen is op jaarbasis, over de periode 1 juli - 30 juni, berekend. Naar telgegevens van het Staatsbosbeheer.

ton was). De sterke afname van het aantal schol en bot (*cf.* Hoofdstuk 3) zal echter wel gepaard zijn gegaan met een geringere predatie door deze groep, waardoor er in principe een groter deel van de grondel-produktie beschikbaar is gekomen voor de visetende vogels. Er is helaas niets bekend over de voedselvoorkeur van de aalscholvers in het Grevelingenmeer.

Terwijl in 1981/1982 de totale jaarlijkse viskonsumptie door vogels op 115 ton VG (0,18 g ADG.m^{-2}) werd geschat, zal dit vermoedelijk zijn toegenomen tot ca. 257 ton (0,4 g ADG.m^{-2}) in 1984/1985. Er zijn dus sterke aanwijzingen, dat de invloed van de visetende vogels op de visfauna (inklusief epibenthische crustaceeën zoals garnalen) van het Grevelingenmeer sterk is toegenomen. Naar de wijze waarop de visfauna op deze toegenomen predatie heeft gereageerd kan alleen maar worden geraden. Aangezien naar schatting in 1981/1982 tenminste 60% van de in de nazomer aanwezige grondels door platvissen en vogels werd weggegeten, lijkt er voorlopig op basis van de beschikbare schattingen geen ruimte te zijn voor een verdere uitbreiding van de predatie door vogels zonder dat dit ernstige gevolgen voor de grondelpopulaties heeft.

Tenslotte is in Tabel 4 een algemeen overzicht gegeven van de geschatte biomassa's, jaarlijkse produktie- en oogstcijfers (vangsten en/of konsumpties) van de verschillende vissoorten in het Grevelingenmeer gedurende de periode 1980 - 1982. Tegenwoordig wordt de visfauna gedomineerd (op basis van gewicht) door aal *Anguilla anguilla*, terwijl de schol *Pleuronectes platessa* naar de tweede plaats is teruggevallen. In het vroegere Grevelingen estuarium en direkt na de afsluiting werd de biomassa van de bodemvissen overheerst door die van schol (Vaas, 1979).

Slechts 25% van de totale biomassa wordt geschat te behoren tot de pelagische vissoorten. Driedoornige stekelbaars *Gasterosteus aculeatus*, sprot *Sprattus sprattus* en koornaarvis *Atherina* sp. planten zich in het meer voort (Doornbos, 1981, 1982), terwijl wordt aangenomen, dat de haring *Clupea harengus* populatie direkt afhankelijk is van de intrek van jonge haring door de Brouwerssluis tijdens de winter.

Volgens de door Jansson *et al.* (1985) bijeengebrachte gegevens uit de literatuur kan in kustgebieden de biomassa van de visfauna oplopen tot 125 g VG.m^{-2}, terwijl de jaargemiddelden ruwweg tussen de 0,2 - 17 g VG.m^{-2} variëren. Daarmee vergeleken is de 7,1 g VG ($\sim$ 1,2 g ADG).m^{-2}, zoals gevonden voor het Grevelingenmeer, een intermediaire waarde (Tabel 4).

Tabel 4. Globale schatting van biomassa, jaarlijkse produktie en opbrengst (*c.q.* konsumptie) van de belangrijkste vissoorten in het Grevelingenmeer gedurende 1980 - 1982 (de cijfers zijn in tonnen versgewicht en slaan op het totale gebied, zijnde 108 km^2). Indien bekend, zijn ook de belangrijkste konsumenten van de vissen genoemd.

Soort	Biomassa	Produktie	Opbrengst / Konsumpt.	Belangrijkste konsumenten
Bodemvissen				
Pleuronectes platessa	125		20	Mens (sportvissers)
Platichthys flesus	60		10	Mens (sportvissers)
Overige Pleuronectiformes	35			
Anguilla anguilla	170	> 85	85	Mens, vogels?
Pomatoschistus microps	72	261		
Pomatoschistus minutus	85	271	102[1]	Platvissen, vogels
Gobius niger	15	∿ 48		
Pelagische vissen				
Gasterosteus aculeatus	∿ 40		2,4[1]	Vogels
Sprattus sprattus	∿ 70		3,3[1]	Vogels
Clupea harengus	∿ 70		9,9[1]	Vogels, sportvissers?
Atherina sp.	∿ 22		0,4[1]	Vogels
Totaal	764	= 7,1 g $VG.m^{-2}$		

1) Betreft alleen gegevens van 1980/1981

Epiloog

Tien tot vijftien jaar na de afsluiting is de ontwikkeling van het oecosysteem van het zoute Grevelingenmeer nog volop in beweging en is er nog weinig sprake van een stabilisatie rond een duidelijk evenwicht. Dit geldt niet alleen voor zaken als primaire produktie (Nienhuis, 1985) en macrozoöbenthos (Lambeck, 1985), maar zeker ook voor de visfauna.

Met betrekking tot de rol van de vissen in het meer kunnen, op basis van het onderhavige onderzoek, een aantal konklusies worden getrokken:

1. Het aantal vissoorten in het Grevelingenmeer is betrekkelijk gering.
2. Er zijn slechts weinig vissen die op macrozoöbenthos en kleine prooivissen prederen.
3. Een aantal vissoorten, die uitstekend in het zoutwatermeer kunnen leven, slagen er niet in zich met succes voort te planten en zijn afhankelijk van de intrek van larven en juvenielen om zich als populatie te kunnen handhaven.
4. In de voedselketen van het meer nemen de grondels een sleutelpositie in. Kwantitatief vormen zij de belangrijkste schakel in de energieoverdracht van de lagere trophische niveaux naar de hogere.

De verwachtingen omtrent de toekomstige ontwikkelingen van de visstand in het Grevelingenmeer blijven noodgedwongen erg spekulatief van aard. Veel zal afhangen van het te voeren sluisbeheer. Sinds 1983 kan de beheerder, behalve met de Brouwerssluis, eveneens met de Flakkeese spuisluis manipuleren, waardoor een kunstmatig stromingspatroon (bijvoorbeeld van west naar oost) kan worden opgewekt. De visstand kan direkt worden beïnvloed door een gericht sluisbeheer, zij het waarschijnlijk op beperkte schaal.

Tot nu toe zijn een aantal voorstellen gedaan om de visstand ten behoeve van het beroepsmatige en rekreatieve (sportvisserij) gebruik te verbeteren (*cf.* Steinmetz & Slothouwer, 1979; Doornbos, 1985; Klein Breteler, 1986; Klein Breteler & Steinmetz, 1987). Aangezien de natuurlijke intrek van glasaal gering is, is getracht om jaarlijks ca. 2500 kg glasaal en/of pootaal in het meer uit te zetten teneinde de verliezen tengevolge van natuurlijke sterfte, predatie (door aalscholvers?) en wegtrek van de waardevolle schieraal in het najaar te kompenseren, en om de opbrengsten voor de beroepsvisserij te verbeteren. Door schaarsheid van glasaal en pootaal op de Europeese markt kan dit streefgetal echter niet elk jaar worden gehaald. Een verdere toename van de aalvangsten door de beroepsvissers ligt in de nabije toekomst dan ook niet in de lijn der verwachtingen.

Door in het voorjaar tot aan het einde van april rond hoogwater Noordzee-water in te laten met behulp van de Brouwerssluis en het overtollige meerwater tijdens laagwater te spuien via de hevel in de Grevelingendam kunnen er zoveel mogelijk schollarven naar binnen worden gespoeld. Deze hebben verder weinig problemen om zich definitief in het meer te vestigen. De Brouwerssluis zou tot eind januari gesloten moeten blijven om wegtrek van oudere schol zoveel mogelijk tegen te gaan. Wanneer om bepaalde redenen, bijvoorbeeld vanwege de waterkwaliteit, toch Noordzeewater moet worden ingelaten gedurende de herfst of winter, dan zou dat bij voorkeur moeten gebeuren bij stroomsnelheden boven de 1,5 $m.s^{-1}$, overeenkomend met de hoogste zwemsnelheden die volwassen schol gedurende langere tijd kan volhouden.

Op basis van een aantal aannames zijn schattingen gemaakt betreffende de mogelijke bestandsontwikkelingen en de door sportvissers te vangen hoeveelheden schol (Fig. 6). Uit deze modellen blijkt, dat, wanneer de jaarlijkse intrek en sterfte konstant worden gehouden, er na tien tot vijftien jaar een evenwichtssituatie ontstaat in het aantal oudere schol. Bij een intrek van bijvoorbeeld 2 miljoen larven per jaar mag een bestand van ongeveer 0,6 miljoen oudere schol ($\geqslant$ 1 jaar) worden verwacht, waarvan slechts 270.000 stuks een leeftijd van drie jaar of ouder zullen bereiken. In geval van een jaarlijkse intrek van 5 miljoen larven zullen deze waarden oplopen tot respektievelijk 1,5 en 0,7 miljoen stuks (Fig. 6a). Aangezien er door de Brouwerssluis in het voorjaar ook een onbekend aantal I-groep schol naar binnen trekt, zou het evenwicht in de praktijk iets hoger kunnen liggen dan wanneer wordt uitgegaan van een intrek van uitsluitend larven.

Aangezien de wettelijke minimum maat voor schol in Nederland tegenwoordig 27 cm is en deze lengte in het Grevelingenmeer in het derde levensjaar wordt bereikt (*cf.* Doornbos & Twisk, 1984), kan ook het aantal door de sportvissers te vangen schol worden berekend. De verwachting lijkt gerechtvaardigd, dat er bij een jaarlijkse intrek van 2 tot 5 miljoen larven ca. 60.000 tot 160.000 volwassen schollen per jaar kunnen worden gevangen (Fig. 6b).

Aangezien in de periode 1979 - 1985 slechts één keer het aantal

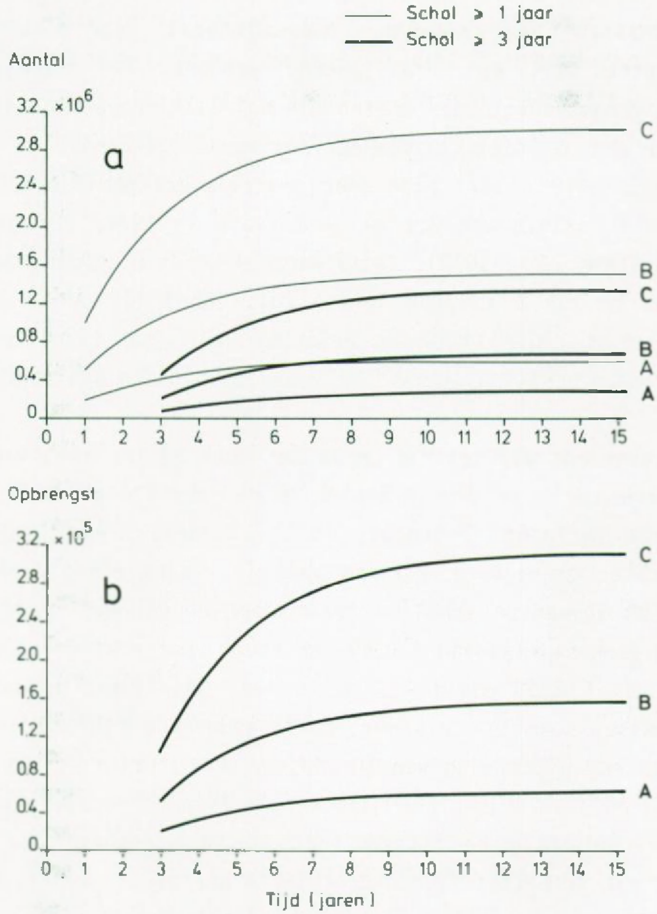


Fig. 6. Drie modellen met betrekking tot de te verwachten bestandsontwikkeling van de oudere scholpopulatie in het Grevelingenmeer (a) en het aandeel van drie jaar en oudere schol dat daarvan door sportvissers geoogst zou kunnen worden (b). In de modellen A, B en C is aangenomen dat er jaarlijks gedurende het voorjaar een intrek is van respektievelijk 2, 5 en 10 miljoen schollarven en dat het de overlevende schol wordt belet om het meer in de herfst en winter te verlaten. Verder is er van uitgegaan dat de mortaliteit onder juveniele schol (< 1 jaar) 90% per jaar en onder oudere schol 33% per jaar is. De visserijsterfte is gesteld op gemiddeld 23% per jaar.

binnentrekkende larven op 10 miljoen individuen werd geschat (Tabel 1), lijkt het onwaarschijnlijk dat gedurende 10 tot 15 jaar achter elkaar een zo grote intrek tot de mogelijkheden behoort. De daarbij behorende bestands- en vangstschattingen moeten dan ook als irreëel worden beschouwd, zelfs wanneer een optimaal sluisbeheer zou worden gevoerd.

Gedurende 1972 - 1977 zijn door sportvissers gemiddeld 1,25 miljoen schol, met een maximum van 3,1 miljoen stuks in 1974, per jaar gevangen (Steinmetz & Slothouwer, 1979). Zelfs wanneer wordt uitgegaan van een optimistische intrek van 5 miljoen larven (*cf.* Tabel 1), dan moet de sportvisserij rekening houden met een relatief lage jaarlijkse opbrengst van 160.000 volwassen schollen. Het is de vraag of dit een aantrekkelijk alternatief is.

Er is eveneens voorgesteld om in het meer kleine scholletjes met een lengte van ongeveer 5 cm uit te zetten en de oudere platvis te verhinderen het gebied te verlaten (Doornbos, 1985). Volgens Klein Breteler (1986) zouden er echter ongeveer 1 miljoen van die visjes nodig zijn om uiteindelijk 200.000 volwassen schollen te kunnen vangen. Dit houdt in, dat er bij een huidige kostprijs van f 0,50 per stuk, voor elke gevangen schol een investering van f 2,50 nodig is. Om tot een jaarlijkse vangst van ca. 2 miljoen volwassen schollen te komen, zoals gedurende 1973 en 1974 gebruikelijk was, zou een uitzetting van 10 miljoen scholletjes en een investering van rond de 1 miljoen gulden per jaar vergen (Klein Breteler, 1986).

Zeer recent zijn er besprekingen op gang gekomen om in het meer zalmachtigen uit te zetten (Klein Breteler & Steinmetz, 1987). Jonge regenboogforel *Salmo gairdneri* (20 - 25 cm), "smolts" van zeeforel *S. trutta trutta* (15 - 20 cm) of zalm *S. salar* (10 - 16 cm), of een kombinatie van deze drie soorten, zouden het beste in het voorjaar kunnen worden uitgezet nadat de Brouwerssluis zou zijn gesloten. Op deze manier wordt een wegtrek van de vissen naar de Noordzee tegengegaan. Aangezien de "smolts" na ongeveer twee maanden hun trekdrang verliezen, zal vermoedelijk slechts een gering aantal vissen in de herfst proberen het meer te verlaten, zodat het huidige sluisbeheer kan blijven gehandhaafd.

Op basis van een schatting van een voedselaanbod van 1400 à 1800 ton VG voor de zalmachtigen in het meer en uitgaande van een algehele voedselkonversie van 5, zou een jaarlijkse produktie van zalmachtigen van 300 à 350 ton haalbaar moeten zijn (Klein Breteler & Steinmetz, 1987). Zij berekenden ook, dat, bij een maximale uitzetting van 20 - 60 "smolts" per ha.j^{-1} (afhankelijk van de soort), de sportvissers ten hoogste 100.000 à 200.000 forellen of 70.000 à 150.000 zalmen per jaar zouden kunnen vangen. Wanneer er regenboogforel wordt uitgezet, zou ongeveer 75% van de vangst uit volwassen vissen met een lengte van 40 - 45 cm (0,5 - 1 kg) kunnen bestaan, terwijl in het geval van de zalm ca. 75% van de vissen een lengte van 45 - 55 cm (1 - 2 kg) zou hebben en 25% zelfs een lengte kunnen bereiken van 65 - 75 cm (3 - 4 kg) of mogelijk nog wat groter kunnen zijn. De jaarlijkse kosten worden voor forel op 1 à 1,5 miljoen gulden en voor zalm op 1,5 à 2 miljoen gulden geraamd. Daartegenover staat echter een geschatte opbrengst (bijvoorbeeld van visakten en de verkoop van vis door de beroepsvissers) van ca. 1,5 à 2 miljoen gulden bij de uitzetting van forel en zelfs 4 à 5 miljoen in het geval van zalm. Op basis hiervan komen zij tot de konklusie, dat de uitzetting van zalm het meest winstgevend zou zijn. Anderzijds zouden in strenge winters de overlevingskansen van de zalmachtigen (en met name zalm) in het zoutwatermeer sterk verminderd kunnen worden door de lage watertemperaturen. Ook zou in warme zomers de watertemperatuur een kritische waarde kunnen overschrijden (Klein Breteler & Steinmetz, 1987).

Vooralsnog zijn de diskussies over de verbetering van de visfauna van het Grevelingenmeer nog niet afgesloten, met name binnen de werkgroep "Salmoniden in het Grevelingenmeer", waarin verschillende specialisten zitting hebben (Klein Breteler & Steinmetz, 1987). Er zal echter nog veel gericht experimenteel onderzoek nodig zijn, voordat een doelmatig beleid ten aanzien van het beheer van de visstand in het Grevelingenmeer kan worden verwezenlijkt en als gevolg daarvan ook de eerste tastbare resultaten kunnen worden verwacht.

Literatuur

Andrews, M.J., 1984. Thames estuary: pollution and recovery. In: P.J. Sheehan, D.R. Miller, G.C. Butler & P. Bourdeau. Effects of pollutants at the ecosystem level. John Wiley and Sons, New York: 195-227.

Anonymus, 1982. Project 1-7090 - Bestandsbepalingen jonge platvis en garnaal. Visserij *35*: 162-164.

Anonymus, 1984. Project 1-7090 - Bestandsbepalingen jonge platvis en garnaal. Visserij *37*: 232-233.

Anonymus, 1985. Report of the 0-group North Sea flatfish working group, IJmuiden, 21 - 25 November 1983. ICES Demersal Fish Committee C.M. 1985/G:2: 1-96.

Bamber, R.N. & P.A. Henderson, 1985. Morphological variation in British atherinids, and the status of *Atherina presbyter* Cuvier (Pisces: Atherinidae). Biol. J. Linn. Soc. *25*: 61-76.

Bannink, B.A., J.H.M. van der Meulen & P.H. Nienhuis, 1984. Lake Grevelingen: from an estuary to a saline lake. An introduction. Neth. J. Sea Res. *18*: 179-190.

Bardach, J.E., J.H. Ryther & W.O. McLarney, 1972. Aquaculture. The farming and husbandry of freshwater and marine organisms. Wiley-Interscience, New York: 1-868.

Beaumont, W.R.C. & R.H.K. Mann, 1984. The age, growth and diet of a freshwater population of the flounder, *Platichthys flesus* (L.), in southern England. J. Fish Biol. *25*: 607-616.

Claridge, P.N., I.C. Potter & M.W. Hardisty, 1986. Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn estuary. J. mar. biol. Ass. U.K. *66*: 229-258.

Doornbos, G., 1981. Verwachtingen voor de ontwikkeling van de visstand in een zoute of zoete Grevelingen tegen de achtergrond van de veranderingen die zijn opgetreden in de visfauna in de periode 1960 - 1980. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 81 III 6: 1-28.

Doornbos, G., 1982. Changes in the fish fauna of the former Grevelingen estuary, before and after the closure in 1971. Hydrobiol. Bull. *16*: 279-283.

Doornbos, G., 1985. Vissen in de Grevelingen. In: P.H. Nienhuis. Het Grevelingenmeer. Van estuarium naar zoutwatermeer. Delta Instituut voor Hydrobiologisch Onderzoek/Natuur en Techniek, Yerseke/ Maastricht-Brussel: 130-145.

Doornbos, G. & F. Twisk, 1984. Density, growth and annual food consumption of plaice (*Pleuronectes platessa* L.) and flounder (*Platichthys flesus* (L.)) in Lake Grevelingen, The Netherlands. Neth. J. Sea Res. *18*: 434-456.

Doornbos, G., F. Twisk, K.F. Vaas & P. de Koeijer, 1981. De visfauna van de open Oosterschelde: een inventarisatie over de periode 1960 - 1976. Rapporten en Verslagen Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, nr. 1981-5: 1-55.

Doornbos, G., F. Twisk & R.H. Bogaards, 1986. Kwantificering van vissen. ZOWEC III, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 86 III 5: 1-190.

Duursma, E.K., H. Engel & T.J.M. Martens (red.), 1982. De Nederlandse Delta. Een compromis tussen milieu en techniek in de strijd tegen het water. Natuur en Techniek, Maastricht: 1-511.

Duursma, E.K. & E.S. Nieuwenhuize (hoofdred.), 1985. Delta Institute for Hydrobiological Research, Progress Report 1984. Delta Institute for Hydrobiological Research, Yerseke: 1-83.

Fonds, M., 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In: E. Naylor & R.G. Hartnoll. Cyclic phenomena in marine plants and animals. Proc. 13th Eur. Mar. Biol. Symp., Isle of Man, Great Britain. Pergamon Press, Oxford: 151-156.

Goossens, J.G.C.M., R.S. Minnaar & J.C. Verplanke, 1983. Koolstofmineralisatie in het water van het Grevelingenmeer. ZOWEC I, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 I 5: 1-35.

Hartley, P.H.T., 1940. The Saltash tuck-net fishery and the ecology of some estuarine fishes. J. mar. biol. Ass. U.K. *24*: 1-68.

Ierland, E.T. van & L. Peperzak, 1982. Scheiding van seston. ZOWEC V, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 82 V 5: 1-127.

Jansson, B.-O., G. Aneer & S. Nellbring, 1985. Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census. Mar. Ecol. Prog. Ser. *23*: 31-43.

Kelderman, P., 1983. Bodem-water uitwisseling in de Grevelingen. ZOWEC IV, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 IV 5: 1-110.

Klein Breteler, P.H.M., 1986. Prognoses voor de ontwikkeling van de scholstand in een zoute Grevelingen. Visserij *39*: 16-31.

Klein Breteler, P.H.M. & B. Steinmetz, 1987. Toekomstig visstandbeheer in een zout Grevelingenmeer. Nota Werkgroep Salmoniden Grevelingenmeer: 1-52.

Roem is het Riek

Roem is het riek
van dei kerel op diek.
Luddek de zichter,
groot is de dichter,
Hoog is de lucht
mit zien zeewolkenvlucht.
Wiedweg de robben,
stoefbie de kobben,
Braid is het pad,
dat doar wenkt over 't Wad.
't Pad van de struner,
't laand van de nuner,
Naarms gain grens
veur zien endloze wens...

Uit de bundel *"Zun, Wiend en Wolken"* (1959)
van de Groninger dichter Jan Boer.

zoek, Yerseke, nr. 1981-5: 1-55.

Doornbos, G., F. Twisk & R.H. Bogaards, 1986. Kwantificering van vissen. ZOWEC III, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 86 III 5: 1-190.

Duursma, E.K., H. Engel & T.J.M. Martens (red.), 1982. De Nederlandse Delta. Een compromis tussen milieu en techniek in de strijd tegen het water. Natuur en Techniek, Maastricht: 1-511.

Duursma, E.K. & E.S. Nieuwenhuize (hoofdred.), 1985. Delta Institute for Hydrobiological Research, Progress Report 1984. Delta Institute for Hydrobiological Research, Yerseke: 1-83.

Fonds, M., 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In: E. Naylor & R.G. Hartnoll. Cyclic phenomena in marine plants and animals. Proc. 13th Eur. Mar. Biol. Symp., Isle of Man, Great Britain. Pergamon Press, Oxford: 151-156.

Goossens, J.G.C.M., R.S. Minnaar & J.C. Verplanke, 1983. Koolstofmineralisatie in het water van het Grevelingenmeer. ZOWEC I, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 I 5: 1-35.

Hartley, P.H.T., 1940. The Saltash tuck-net fishery and the ecology of some estuarine fishes. J. mar. biol. Ass. U.K. *24*: 1-68.

Ierland, E.T. van & L. Peperzak, 1982. Scheiding van seston. ZOWEC V, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 82 V 5: 1-127.

Jansson, B.-O., G. Aneer & S. Nellbring, 1985. Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census. Mar. Ecol. Prog. Ser. *23*: 31-43.

Kelderman, P., 1983. Bodem-water uitwisseling in de Grevelingen. ZOWEC IV, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 IV 5: 1-110.

Klein Breteler, P.H.M., 1986. Prognoses voor de ontwikkeling van de scholstand in een zoute Grevelingen. Visserij *39*: 16-31.

Klein Breteler, P.H.M. & B. Steinmetz, 1987. Toekomstig visstandbeheer in een zout Grevelingenmeer. Nota Werkgroep Salmoniden Grevelingenmeer: 1-52.

Kuipers, B.R., 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. Neth. J. Sea Res. *11*: 56-91.

Lambeck, R.H.D., 1985. Leven zonder getij. Bodemdieren in het Grevelingenmeer. Natuur en Techniek *53*: 916-931.

Lindeboom, H.J. & H.A.J. de Klerk - van der Driessche, 1983. C-mineralisatie op en in de bodem van de Grevelingen. ZOWEC II, Eindrapport. Delta Instituut voor Hydrobiologisch Onderzoek/Rijkswaterstaat DDMI, Yerseke/Middelburg, Nota Z 83 II 5: 1-132.

Meininger, P.L., H.J.M. Baptist & G.J. Slob, 1984. Vogeltellingen in het Deltagebied in 1975/76 - 1979/80. Rijkswaterstaat Deltadienst/Staatsbosbeheer Zeeland, Middelburg/Goes, Nota DDMI-84.23: 1-390.

Meininger, P.L., H.J.M. Baptist & G.J. Slob, 1985. Vogeltellingen in het zuidelijk Deltagebied in 1980/81 - 1983/84. Rijkswaterstaat DGW/Staatsbosbeheer Zeeland, Middelburg/Goes, Nota DGWM 85.001: 1-159.

Nie, H.W. de, 1987. Food, feeding periodicity and consumption of the eel, *Anguilla anguilla* (L.), in the shallow eutrophic Tjeukemeer (The Netherlands). Arch. Hydrobiol. (in druk).

Nienhuis, P.H., 1978a. An ecosystem study in Lake Grevelingen, a former estuary in the SW Netherlands. Kieler Meeresforsch. (Sonderheft) *4*: 247-255.

Nienhuis, P.H., 1978b. Lake Grevelingen: a case study of ecosystem changes in a closed estuary. Hydrobiol. Bull. *12*: 246-259.

Nienhuis, P.H. (red.), 1985. Het Grevelingenmeer. Van estuarium naar zoutwatermeer. Delta Instituut voor Hydrobiologisch Onderzoek/Natuur en Techniek, Yerseke/Maastricht-Brussel: 1-177.

Nijssen, H. & S.J. de Groot, 1980. Zeevissen van de Nederlandse kust. Wet. Med. Kon. Ned. Natuurhist. Ver., Hoogwoud *143*: 1-109.

Philippart, R.J.L. & A.J.M. Meijer, 1982. Monitoring-onderzoek aan de visstand van de Grevelingen: resultaten 1980 - 1981. Bureau Waardenburg B.V., Culemborg: 1-64 (+ Bijlagen).

Rijnsdorp, A.D., M. van Stralen & H.W. van der Veer, 1985. Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. Trans. Am. Fish. Soc. *114*: 461-470.

Steinmetz, B. & D. Slothouwer, 1979. De betekenis van de Grevelingen voor de sportvisserij. Visserijkundige waarnemingen in de jaren 1971 - 1977. Directie van de Visserijen, Den Haag, Documentatierapport no. 21: 1-101.

Summers, R.W., 1979. Life cycle and population ecology of the flounder *Platichthys flesus* (L.) in the Ythan estuary, Scotland. J. nat. hist. *13*: 703-723.

Vaas, K.F., 1970. Studies on the fish fauna of the newly created lake near Veere, with special emphasis on the plaice (*Pleuronectes platessa*). Neth. J. Sea Res. *5*: 50-95.

Vaas, K.F., 1979. Studies on the fish fauna of an estuary in the S.W. Netherlands, before and after its change into the stagnant, saline, Lake Grevelingen. Hydrobiol. Bull. *13*: 177-188.

Veer, H.W. van der, 1985. Impact of coelenterate predation on larval plaice *Pleuronectes platessa* and flounder *Platichthys flesus* stock in the western Wadden Sea. Mar. Ecol. Prog. Ser. *25*: 229-238.

Vlas, J. de, 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. Neth. J. Sea Res. *13*: 117-153.

Waardenburg, H.W., A.J.M. Meijer, R.J.L. Philippart & A.C. van Beek, 1984. The hard bottom biocoenoses and the fish fauna of Lake Grevelingen, and their reactions to changes in the aquatic environment. Wat. Sci. Tech. *16*: 677-686.

Wheeler, A., 1978. Key to the fishes of northern Europe. Frederick Warne Ltd, London: 1-380.

Witte, J.Y. & J.J. Zijlstra, 1978. The species of fish occurring in the Wadden Sea. In: N. Dankers, W.J. Wolff & J.J. Zijlstra. Fishes and fisheries of the Wadden Sea. Final report of the section "Fishes and fisheries" of the Wadden Sea Working Group. Stichting Veth tot Steun aan Waddenonderzoek, Leiden: 10-19.

Wolff, W.J., M.A. Mandos & A.J.J. Sandee, 1981. Tidal migration of plaice and flounders as a feeding strategy. In: N.V. Jones & W.J. Wolff. Feeding and survival strategies of estuarine organisms. Plenum Press, New York: 159-171.

Zijlstra, J.J., R. Dapper & J.IJ. Witte, 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea Res. *15*: 250-272.

Appendix 1. List of fish species observed in Lake Grevelingen during 1979 to 1982. After data of Doornbos (1981), Philippart & Meijer (1982), Waardenburg *et al.* (1984) and unpublished records (*e.g.* A.J.M. Meijer, personal communication).

FAMILY Genus/(Sub)Species	English name	Nederlandse naam	1979	1980	1981	1982
PETROMYZONIDAE						
1. *Petromyzon marinus*	Lamprey	Zeeprik		+	+	+
2. *Lampetra fluviatilis*	Lampern	Rivierprik			+	+
CARCHARHINIDAE						
3. *Galeorhinus galeus*	Tope	Ruwe haai		+		
SQUALIDAE						
4. *Squalus acanthias*	Spurdog	Doornhaai		+		
DASYATIDAE						
5. *Dasyatis pastinaca*	Stingray	Pijlstaartrog		+	+	+
ANGUILLIDAE						
6. *Anguilla anguilla*	Eel	Aal	+	+	+	+
CONGRIDAE						
7. *Conger conger*	Conger	Zeepaling		+	+	
CLUPEIDAE						
8. *Clupea harengus*	Herring	Haring	+	+	+	+
9. *Sprattus sprattus*	Sprat	Sprot	+	+	+	+
10. *Sardina pilchardus*	Pilchard	Sardien				+
11. *Alosa fallax*	Twaite shad	Fint			+	+
ENGRAULIDAE						
12. *Engraulis encrasicolus*	Anchovy	Ansjovis				+
SALMONIDAE						
13. *Salmo trutta trutta*	Sea trout	Zeeforel			+	+
14. *Salmo gairdneri*	Rainbow trout	Regenboogforel	+	+	+	+
15. *Salmo* sp.	"Salmon"	"Zalm"		+	+	+
OSMERIDAE						
16. *Osmerus eperlanus*	Smelt	Spiering		+	+	+
GADIDAE						
17. *Gadus morhua*	Cod	Kabeljauw		+	+	+
18. *Merlangius merlangus*	Whiting	Wijting	+	+	+	+
19. *Pollachius pollachius*	Pollack	Pollak		+	+	+
20. *Pollachius virens*	Saithe	Koolvis		+	+	+
21. *Trisopterus luscus*	Bib	Steenbolk		+	+	+
22. *Raniceps raninus*	Tadpole-fish	Vorskwab	+	+	+	+
23. *Ciliata mustela*	Five-bearded rockling	Vijfdradige meun		+	+	+
ZOARCIDAE						
24. *Zoarces viviparus*	Viviparous blenny	Puitaal	+	+	+	+
BELONIDAE						
25. *Belone belone*	Garfish	Geep	+	+	+	+
ATHERINIDAE						
26. *Atherina boyeri*[1)] (*A. presbyter*)	Sand-smelt	Koornaarvis	+	+	+	+
GASTEROSTEIDAE						
27. *Gasterosteus aculeatus*	Three-spined stickleback	Driedoornige stekelbaars	+	+	+	+
28. *Pungitius pungitius*	Nine-spined stickleback	Tiendoornige stekelbaars			+	
SYNGNATHIDAE						
29. *Syngnathus acus*	Greater pipefish	Grote zeenaald	+	+	+	+
30. *Syngnathus rostellatus*	Nilsson's pipefish	Kleine zeenaald	+	+	+	+
31. *Entelurus aequoreus*	Snake pipefish	Adderzeenaald		+	+	+
TRIGLIDAE						
32. *Trigla lucerna*	Tub gurnard	Rode poon		+	+	+
33. *Eutrigla gurnardus*	Grey gurnard	Grauwe poon			+	

1) Recently Bamber & Henderson (1985) showed that the formerly distinguished individuals of *Atherina presbyter* and *A. boyeri* belong to a single species, *i.e. A. boyeri*.

Appendix 1. (continued)

FAMILY Genus/(Sub)Species	English name	Nederlandse naam	1979	1980	1981	1982
COTTIDAE						
34. *Myoxocephalus scorpius*	Bull-rout	Zeedonderpad	+	+	+	+
35. *Taurulus bubalis*	Sea scorpion	Groene zeedonderpad		+	+	+
AGONIDAE						
36. *Agonus cataphractus*	Hooknose	Harnasmannetje		+	+	+
CYCLOPTERIDAE						
37. *Cyclopterus lumpus*	Lumpsucker	Snotolf		+	+	+
38. *Liparis liparis*	Sea-snail	Slakdolf	+		+	+
SERRANIDAE						
39. *Dicentrarchus labrax*	Bass	Zeebaars	+	+	+	+
CARANGIDAE						
40. *Trachurus trachurus*	Scad	Horsmakreel	+	+	+	+
MUGILIDAE						
41. *Chelon labrosus*	Thick-lipped grey mullet	Diklipharder	+		+	+
42. *Liza ramada*	Thin-lipped grey mullet	Dunlipharder	+	+	+	+
PHOLIDAE						
43. *Pholis gunnellus*	Butterfish	Botervis	+	+	+	+
AMMODYTIDAE						
44. *Ammodytes tobianus*	Sandeel	Zandspiering		+	+	+
45. *Hyperoplus lanceolatus*	Greater sandeel	Smelt			+	+
CALLIONYMIDAE						
46. *Callionymus lyra*	Dragonet	Pitvis	+		+	+
GOBIIDAE						
47. *Gobius niger*	Black goby	Zwarte grondel	+	+	+	+
48. *Pomatoschistus microps*	Common goby	Brakwatergrondel	+	+	+	+
49. *Pomatoschistus minutus*	Sand goby	Dikkopje	+	+	+	+
50. *Pomatoschistus pictus*	Painted goby	Kleurige grondel	+	+	+	
51. *Aphia minuta*	Transparent goby	Glasgrondel	+	+	+	
SCOMBRIDAE						
52. *Scomber scombrus*	Mackerel	Makreel		+	+	+
SCOPHTHALMIDAE						
53. *Scophthalmus rhombus*	Brill	Griet	+	+	+	+
54. *Scophthalmus maximus*	Turbot	Tarbot	+	+	+	+
PLEURONECTIDAE						
55. *Pleuronectes platessa*	Plaice	Schol	+	+	+	+
56. *Limanda limanda*	Dab	Schar	+	+	+	+
57. *Platichthys flesus*	Flounder	Bot	+	+	+	+
58. *Microstomus kitt*	Lemon sole	Tongschar		+	+	+
SOLEIDAE						
59. *Solea solea*	Sole	Tong	+	+	+	+
	Total	Totaal	31	48	55	52

Total number of families: 31
Total number of species : 59

Roem is het Riek

Roem is het riek
van dei kerel op diek.
Luddek de zichter,
groot is de dichter,
Hoog is de lucht
mit zien zeewolkenvlucht.
Wiedweg de robben,
stoefbie de kobben,
Braid is het pad,
dat doar wenkt over 't Wad.
't Pad van de struner,
't laand van de nuner,
Naarms gain grens
veur zien endloze wens...

Uit de bundel "*Zun, Wiend en Wolken*" (1959)
van de Groninger dichter Jan Boer.

Dei hier aas kiend al kwam op diek en kweller
En laans de lien van bloas- en zeewier laip,
Dei luusterde noar wiend as zien verteller
En dei de vogels ien heur vlucht beraip,
Dei mit de wolken al moar wieder voarde
Noar 't wonnerstee, dat veur gain mens bestait,
Dei wer gewoar, wat nooit ien hom bedoarde,
De laifde veur dit laand, ien ainzoamhaid.

Laatste vers van "*Waddenlaand*" uit de bundel
"*Roemte en Voart*" (1954) van de Groninger dichter Jan Boer.