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Competitive food exploitation of smelt *Osmerus eperlanus* by great crested grebes *Podiceps cristatus* and perch *Perca fluviatilis* at Lake IJsselmeer, The Netherlands

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Abstract. The impact of predation by an avian predator (great crested grebe *Podiceps cristatus*) and a predatory fish (perch *Perca fluviatilis*) on a common resource, the small planktivorous fish smelt (*Osmerus eperlanus*) was studied in Lake IJsselmeer, The Netherlands, in July–October 1985–1988. At this time of the year the grebes are in simultaneous wing-moult and therefore temporarily flightless. Four factors limit the predation pressure by grebes: (1) an underwater visibility threshold of c. 40 cm Secchi depth is the lower limit at which large numbers attend the moulting site, (2) a lower density threshold of exploitable smelt biomass of c. 30 kg/ha determines the actual fishing areas, (3) a fish size threshold of 6.5 cm total length further limits prey availability, and (4) the vertical movements of the prey impose a strong (diel) time constraint on the birds, allowing only crepuscular foraging. Perch, the other main predator in this system, is less restricted in its foraging. Perch were found to be in direct competition with the grebes, preying heavily on the juvenile smelt. Over the 4 years of study 90% of all predation from 15 July to 15 October (72–233 kg/ha) was due to perch. The high level of predation by birds and fish was only possible due to a continuous immigration of smelt into the area (1.45 kg/ha per day). In three of the four years, however, the combined predation by fish and birds surpassed the immigration rate of the prey, which led to a strong reduction in smelt stocks in the study area. A conceptual model is developed to describe the different sets of constraints on the grebes' foraging. First, the state of eutrophication in relation to the weather condition determines the degree of algal blooms, and thus underwater visibility, in late summer. This is the major factor governing the numbers of grebes on the moulting area. Second, the size of the population of predatory fish determines the overall food availability (biomass and size distribution of smelt). These factors are partly intercon-

nected and related to human action (pollution, fisheries). It is suggested that, despite deteriorating visibility conditions, the largest moulting site for grebes in Europe at Lake IJsselmeer exists because the stocks of predatory fish are kept low by overfishing.

Key words: Great crested grebe – Perch – Foraging – Predation pressure – Smelt

Several studies have addressed the competition between fish and birds for invertebrate prey (Eriksson 1979; Eadie and Keast 1982; Andersson 1984; Hunter et al. 1986; Hurlbert et al. 1986; Hill et al. 1987; Beattie and Nudds 1989). This study is the first to compare the predatory impacts made by a bird species (great crested grebe *Podiceps cristatus*) and a predatory fish (perch *Perca fluviatilis*) on their main planktivorous fish prey (smelt *Osmerus eperlanus*).

Studies modelling the ecological interactions between birds and fish suggest that the impact of predation by birds on fish populations may in some circumstances be significant (Wiens and Scott 1975; Furness 1978; Furness and Cooper 1982; Bourne 1983; Nettleship et al. 1984; Doornbos 1984). Few empirical studies deal with the assessment of prey availability, or determination of the lowest exploitable prey densities under field conditions. Bird populations which are limited in their movements over a foraging area by the need to return frequently to a central place, colony breeders for example, will exert a relatively high predation pressure on the food resources in the immediate vicinity of the central place (Ashmole 1971; Pearson 1968; Furness 1978, 1990). Great crested grebes assemble on inshore shallows while they undergo their annual wing-moult on Lake IJsselmeer (Piersma et al. 1986; Piersma 1987), during which time they become temporarily flightless since all flight-feathers are replaced simultaneously. Twice a day, at dawn and at dusk, the grebes make foraging trips to offshore waters to feed. The feeding periods coincide with the time of the day when their fish prey are found in the uppermost part of the water column (Piersma et al. 1988).

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Here we first describe the grebes' daily movements, feeding range and diet and the availability of the fish prey populations. This study emphasizes the relationship between fish-eating birds and predatory fish, investigating the possibility of food competition between these two predator groups.

Study area

The work was carried out during July–October 1985–1988 at Lake IJsselmeer, The Netherlands. South of the mainland shore of Friesland (52°50'N, 5°28'E), the Vrouwenzand shallows (<1 m water depth) serve as a roosting site for great crested grebes (Piersma 1987). Further offshore the water depth increases gradually up to 5 m. Blooms of blue-green algae are a regular phenomenon during late summer (Berger and Sweers 1988). The bottom is predominantly sandy and wave action and dense algal populations cause low transparency of the water during summer (average Secchi depth: 40–80 cm). Additional data were collected at Enkhuizerzand (52°39'N, 5°21'E), the other (but less important) moulting area in the southern part of the lake. Here turbidity due to wave-induced transport of silt causes even lower transparencies during summer (max. 20–50 cm Secchi depth). The eutrophic state of the lake results in the fastest growth of cyprinid and percid fish known in The Netherlands (Willemsen 1983).

Methods

Abundance and activity of grebes

Great crested grebes were observed directly from the shore, from an elevated hide next to the reed beds and from vessels. A 15–60 X telescope and a tally counter were used to count the birds. Nocturnal observations were made from the hide with a light intensifier (magnification 2.5–5 X). Further information on the offshore distribution, daily movements and behaviour of the birds was collected during the fishing trips in the years of study, during monthly aerial surveys in 1980–1988, and by recording on ship radar the movements of individual birds and small groups swimming on the flat water surface during the still night of 17–18 September 1986 (see Piersma et al. 1988).

Sampling the fish population

The fish population was sampled with a 15 m long beam trawl, with an opening 7 m wide and 1.2 m high. Mesh width decreased from 45 mm (stretched) near the mouth of the net to 15 mm at the cod end. In addition, a 2-mm mesh 1.5 m long collecting bag was mounted over the end of the net to ensure that the smallest fishes were adequately sampled. The net was towed along the bottom by adding 60-kg iron chain weights to the front of the trawl. Without these weights the trawl sampled the upper water layer, just under the water surface. Towing speed was kept constant at 5 km/h. Fishing was done on fixed transects, 1–4 km long parallel to the shore (see Piersma et al. 1988). Positions were taken from the Trident radio beacon system allowing a precision to less than 5 m. Each transect was fished along the bottom and along the surface, taking care not to cover exactly the same pathway in successive tows on one day. As well as the catching gear, a fish sounder (Lowrance X16) was mounted 2 m away from the side of the ship just under the water

surface, in order to describe the density and vertical distribution of the most common species, smelt, over larger distances.

After sorting and weighing the fish on board, the total lengths of fish in subsamples (>100 individuals) were measured to the nearest 0.5 cm. To estimate the biomass of smelt present, the catches were transformed into kg/ha over the entire water column of 4 m, adding bottom and surface catch and multiplying the total by 2. According to echo-sounding records run simultaneously with the catches, gear efficiency for smelt was determined at 90%. For the assessment of perch stocks we used bottom catches only, assuming a regular distribution over three-quarters of the water column, because this species hardly occurred in the surface catches. We furthermore assumed that catchability is related to a fish's swimming performance, which in turn depends on its size and morphology and the water temperature (Wardle 1983; Bayley 1985). On the basis of the data of Turnpenney and Bamber (1983) for sand smelt *Atherina presbyter*, maximum swimming speed of a 6 cm long smelt at a water temperature of 18 °C would be 33.5 cm/s. For *Micropterus salmoides*, which is related to perch, Beamish (1970) determined a maximum swimming speed of 60 cm/s (18 °C, 25 cm). Endurance time, i.e. the time for which a fish can maintain its maximum swimming speed, is also related to size. According to Beach (1984) this would be 4 s for a 25-cm perch and 1 s for a 6-cm smelt. The multiple of maximum swimming speed and endurance time was used as a relative chance of escape. Larger perch of c. 25 cm thus would be $60 \times 4 / 33.5 \times 1 = 7.16$ times faster than smelt. The catchability for perch was then assumed to be proportional to the difference in swimming performance relative to smelt. This gives a figure of $90 / 7.16 = 12.6\%$ gear efficiency, the value used in this study.

Prey choice and diet

The shyness of the birds and the poor light conditions at the time of feeding made it impossible to quantify the foraging behaviour and intake of the grebes by direct observations on the open water. Instead, food composition and relative intake was estimated from an analysis of the stomach contents of c. 50 grebes that had drowned in fishing nets in the study area in the period 1 August–15 October 1978–1986. No fish remains were found in the oesophagi of grebes at this time of the year. Details of processing of stomach contents and estimating food composition from otoliths and pharyngeal bones, are given by Piersma (1988a). In view of the slight wear of the otoliths of smelt, it was necessary to correct the equation used to predict fish length (FL, cm) from otolith length (OL, mm). The equation used here is $FL = 2.79 OL + 1.9$ ($r^2 = 0.96$, $n = 129$, $P < 0.001$). In August 1987 and 1988 the gullets of freshly caught perch were examined for prey. The total lengths of individual prey fishes were measured.

Predation pressure by perch

Consumption of smelt by perch was estimated from abundance of perch on the study site assuming a regular distribution of fish, and from length changes through the sampling period. For each length class (l) the daily food intake was estimated by the following predictive equation, based on energy requirements for maintenance and growth (M. Fonds pers. comm.):

$$E_l = A \exp 0.1(T - 5) \times W^{0.75} + (1.72 \times G)$$

where: E_l = gross energy intake per length class l (in kJ)
 A = a constant of 0.05 (derived from Solomon and Brafield 1972),
 T = average water temperature (in °C); assuming no temperature effect below 5 °C,
 W = fresh mass (in g),
 G = growth (in kJ); the factor 1.72 stands for $1/0.579$ or $1/\text{net food conversion coefficient}$, the value derived from experiments by Solomon and Brafield (1972).

Totalling average number per size category gives the energy consumption per length class for maintenance; energy required for

growth was then added using the shift in length frequency distributions between sampling periods, and average data in Willemsen (1977). The summation of these values over all size classes leads to an estimate of gross energy intake of all perch present. To convert this into the biomass of smelt eaten per interval we used a metabolizable energy content of 4.5 kJ per g fresh mass (pers. obs.). All data were expressed as fresh mass of smelt eaten (kg/ha).

Predation pressure by grebes

Data on bird numbers and foraging area on the lake were used in order to calculate predation pressure per unit area. Average bird number was calculated over the same intervals as set by the fishing programme, using interpolation between the actual counts. To convert bird numbers into predation pressure an average intake of 85 g smelt per grebe per day was used (Piersma 1988b).

Transparency data

Data on the transparency of the water at different locations and during different periods were provided by the Secchi disc values reported in the WORSRO-data base of Rijkswaterstaat (RIZA, Lelystad).

Results

Abundance and activity patterns of grebes

The number of great crested grebes on the daytime roost increased from early August onwards. Figure 1 shows that the numbers present varied considerably within seasons as well as between years. Peak numbers occurred from the end of August until the beginning of October. The maximum numbers were 8 000, 18 000, 16 000 and 16 000 for

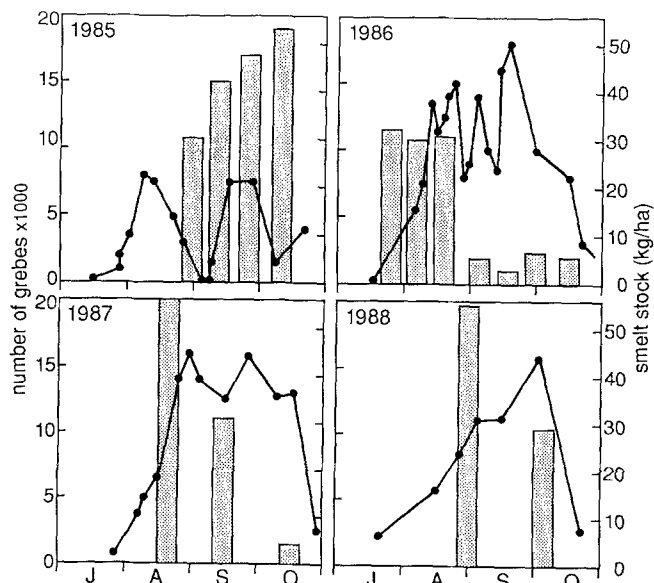


Fig. 1. Total number of great crested grebes attending the daytime roost near the Frisian coast during August–October 1985–1988 (dots). Estimated size of smelt stocks (kg/ha, bars), the grebes' main fish prey at the Vrouwenzand shallows has been indicated. Note the strong decline of smelt stocks in three of the four years

the years 1985–1988 respectively. The average numbers of grebes present between 15 July and 15 October for these years were 4 900, 11 300, 11 300 and 13 500 respectively. Compared to the long-term running mean (1970–1984) of 8 000 grebes (Piersma 1987), the number in 1985 is remarkably low, but the other years showed more grebes than the long-term average.

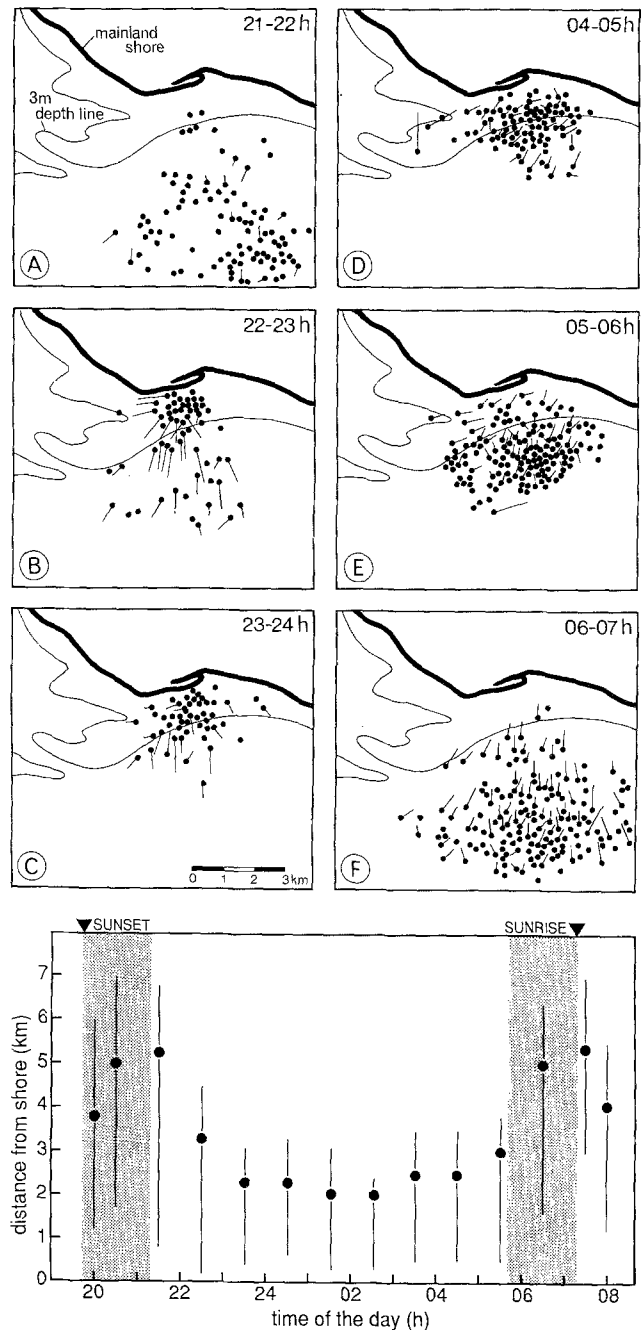


Fig. 2. Selection from a sequence of radar images showing movements of great crested grebes from the roost to their offshore foraging area and back during the night of 16/17 September 1986. From midnight to 04.00 h MET few echos were mapped: most birds stayed close to the shore. The average position and range covered by grebe echos per hour during the course of the night is shown. Grebes reached their greatest distance from the shore during dusk and during dawn (civil twilight). The dots with small bars indicate movements of grebes over an exposure time of 5 min towards the dot

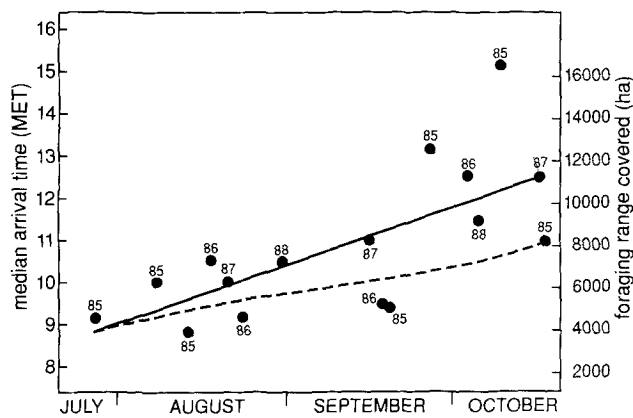


Fig. 3. Median arrival time (MET) in the morning of great crested grebes on their daytime roost in the course of the season. Data from different years have been combined. The lower line shows the time of 4 h after sunrise. Assuming crepuscular foraging and fixed travel speeds, the significantly later arrival relative to sunrise implies a greater feeding range covered by the grebes. Note the late arrival of grebes during the later part of the 1985 season

Great crested grebes in wing-moult leave their coastal roost twice a day to forage in offshore waters. Judging from movements on the radar screen the birds may swim up to at least 7 km on the outward trip. They spread out regularly without gathering in distinct flocks (Fig. 2). The ranges covered by the grebes during 1 day of continuous observation were 5.3 km linear distance during dusk and 5.4 km during dawn. At night the roosting birds stayed on average 2 km from the shore while during daytime they were within 1 km of shore. The average maximum distance from the shore was reached about 1–1.5 h after sunset and 0–1 h before sunrise (Fig. 2). The travel speed of swimming grebes was recorded four times combining radar and shore based observations. The average travel speed was 0.45 m/s (13.9 km covered in 8.5 h, the sum of the measurement intervals).

To estimate the predation pressure we need to know the size of the foraging area. As we could not rely on direct observations, we used the median arrival time (MET) on the roost in the morning to estimate the foraging range.

We know that all birds were foraging until sunrise (Piersma et al. 1988) and then started to move ashore. Figure 3 shows that as the season progresses, grebes returned later in the morning from the foraging area ($r^2 = 0.48$, $P < 0.01$). Relative to sunrise this regression is still significant ($r^2 = 0.30$, $P < 0.05$), indicating that through the season the grebes gradually extended their foraging range. We thus computed foraging range as a function of travel time, assuming a fixed travel speed and regular distribution of the grebes. Foraging ranges of 4 000 ha in late July up to 12 000 ha in mid October were thus estimated. In September and October 1985 the birds apparently covered much larger distances, the reasons for which we will discuss below.

The fish community

A few species dominated the fish community in the waters near Vrouwenzand (Table 1). Smelt was the most numerous species accounting for 40–85% of the numbers caught at various periods. In the upper water layer smelt was even more prominent than along the bottom: >95% of fish biomass and >99% of fish numbers. Smelt were present in two year classes, 0+ and 1+ (Fig. 4). The 1+ cohort was most numerous in summer, in July 1986 contributing up to 24% in terms of numbers. Later in the season less than 8% belonged to this group. This is typical of Lake IJsselmeer. Due to the eutrophic state almost the entire production of smelt is due to fish less than 1 year old (Willemssen 1983).

Ruffe *Gymnocephalus cernuus* and 0+ perch were common, but compared to smelt occurred only in small numbers. Young (0+) bream *Abramis brama* and roach *Rutilus rutilus* were scarce in the study area, contributing less than 0.1% in terms of numbers. On the basis of biomass, large bream were abundant in all years, especially in 1986 when 57.5% of the bottom catches consisted of this species alone (Table 1). Ruffe and perch were very common in 1987. Eel *Anguilla anguilla* was found in some catches, but due to the trawling method was under-represented compared to the other species.

Predatory fish consisted mainly of perch measuring 14–34 cm (2+ and older). Pikeperch *Stizostedion lucio-*

Table 1. Composition by mass (%) of the catches of fish made with the beam trawl over fixed transects in the study area (see Piersma et al. 1988 for details)

Fish species	Bottom trawls				Surface trawls			
	1985	1986	1987	1988	1985	1986	1987	1988
<i>Anguilla anguilla</i>	0.3	0.1	0.2	0.9	<0.1	0.0	0.0	0.0
<i>Osmerus eperlanus</i>	67.6	26.1	23.2	61.3	99.0	97.4	98.5	95.1
<i>Abramis brama</i>	22.3	57.5	29.9	16.6	0.8	2.3	0.2	0.0
<i>Rutilus rutilus</i>	1.1	5.5	10.4	1.6	<0.1	0.1	0.2	0.0
<i>Gasterosteus aculeatus</i>	0.0	1.0	0.0	<0.1	<0.1	<0.1	0.1	<0.1
<i>Gymnocephalus cernuus</i>	2.8	1.9	12.2	7.4	<0.1	<0.1	<0.1	<0.1
<i>Perca fluviatilis</i>	4.7	7.8	22.2	10.6	0.1	0.2	0.2	4.8
<i>Stizostedion lucioperca</i>	1.0	0.9	1.6	1.5	<0.1	<0.1	0.0	0.0
<i>Platichthys flesus</i>	0.2	0.2	0.3	<0.1	<0.1	0.0	0.0	0.0
CPUE	7.50	7.47	12.28	14.85	7.99	6.63	6.70	3.73

All year classes per species were taken together, but the average values for bottom and surface catches are given separately. All catches were made between August and October with the same equipment (4 in 1985, 7 in 1986, 3 in 1987 and 3 in 1988). The presented percentages were weighed for the mass of the individual catches. Average catch per unit effort (CPUE) is given as kg/km trawling

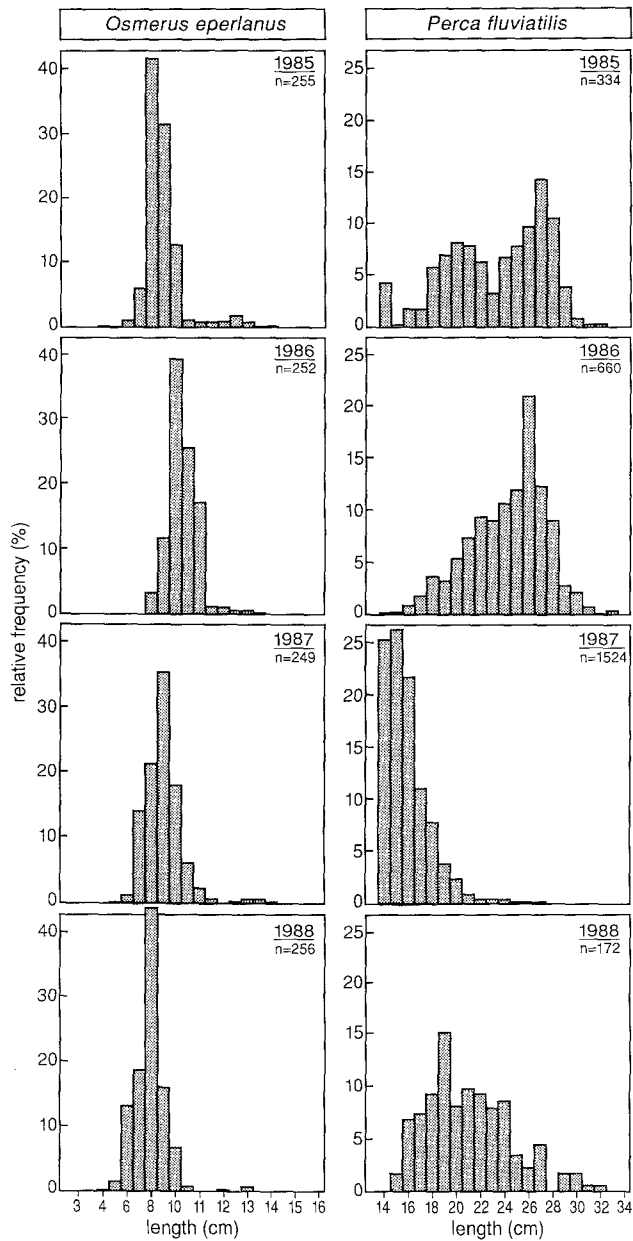


Fig. 4. Frequency distributions of total length of smelt and perch (for the latter species excluding planktivorous 0+ and 1+) in the Vrouwenzand area at the end of the growing season (mid-October) for four different years. Fishery mortality of perch occurs mainly during late autumn and winter, starting when perch reach a total length of 26 cm

perca were extremely scarce (Table 1). Figure 4 shows the size frequency distributions in October of 2+ and older perch which prey on smelt (Willemsen 1983). Large differences occurred between years. In 1985 and 1986 a large part of the perch population studied consisted of individuals exceeding 25 cm (modes of 24 cm and 25 cm respectively). In 1987 and 1988 the perch were much smaller (modes of 15 cm and 21 cm). Over the years the cohort of perch larger than 25 cm disappeared due to commercial fishery in winter.

In the course of the summer smelt grew considerably (Fig. 5). Average length of smelt at the end of the study

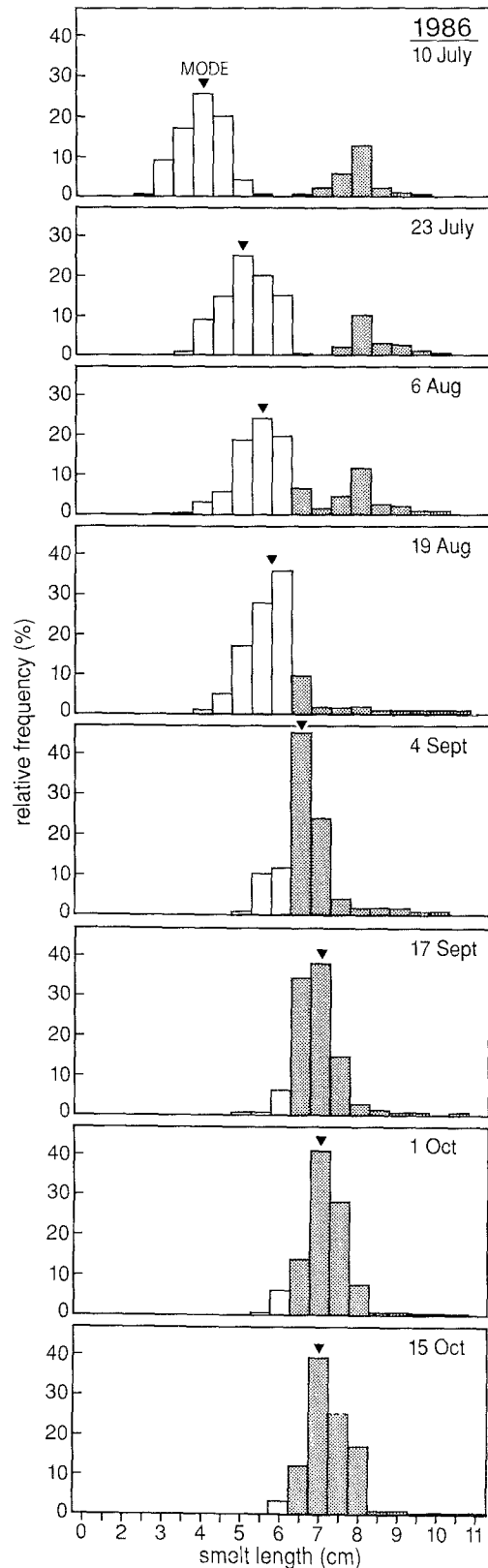


Fig. 5. Growth of smelt in the Vrouwenzand area during the 1986 season. The occurrence of smelt longer than 6.5 cm which are of special importance to the grebes is shown by shaded bars. Note the disappearance of the 1+ cohort during the course of August, which is probably due to avian predation

period (= the growing season) also differed between years (Fig. 4; one-way ANOVA, $F_{3,1008} = 103.55$, $P < 0.0001$). The 0+ group dominated the population in all years of study. In October 1986 average smelt length recorded was highest at 7.24 cm, in 1988 lowest at 5.90 cm (Fig. 4). Average growth rate for 0+ smelt in 1986 was highest at 1.79 mm/week (August–October). For 1+ smelt growth rate was 0.71 mm/week over the same period.

Average catch per unit effort, uncorrected for gear efficiency, was 16.8 kg/km (for all catches surface and bottom trawls combined). Bottom catches accounted on average for 62.7% of the biomass.

Size selection of smelt by grebes and perch

According to stomach contents the diet of the grebes between 1 August and 15 October 1978–1985 was dominated by smelt (96.4% of mass, Piersma et al. 1988). We are able to test for size selection by the grebes since in two cases both the grebe diet (stomach contents of birds drowned in gill nets while foraging) and fish data could be obtained simultaneously. In both examples the moulting grebes took the largest smelt available (Fig. 6). At Enkhuizerzand grebes concentrated almost entirely on the 1+ cohort (7.0–9.5 cm), seeming almost to neglect the abundant 0+ cohort. At Vrouwenzand grebes took preferentially the larger fishes of the 0+ cohort (6.0–7.5 cm) as well as those of the scarce 1+ cohort. Selection for different size classes was computed by Ivlev's selection coefficient E (Jacobs 1974): $E = (r - p)/(r + p)$ where r = fraction of a certain length class taken by the grebes and p = fraction of that length class present in the population. Positive values of E indicate a preference, negative values an underrepresentation. E showed a switchpoint for smelt size at 6.5 cm (Fig. 6C). Smelt larger than this apparent size threshold were ingested more often, smaller smelt less often than expected. This selection pattern also existed when the data were analysed on the basis of mass.

Size selection could not be shown for perch. Instead they preyed mainly on the most abundant size classes of smelt. Stomach analysis of perch in August 1987 and 1988 provided a sample of 51 and 163 smelt respectively, of which the length distribution did not differ significantly from that of the available population (Kolmogorov-Smirnov tests, $D = 0.054$ and 0.044 respectively, both $P > 0.05$). No prey species other than smelt were found.

Predation pressure on smelt by birds and fish

Since smelt is the single most important prey of grebes and perch in the study area, and since it is also the most numerous fish species, we are able to calculate predation pressure on this species in the Vrouwenzand area. Energy requirements for piscivorous perch consist of a maintenance and a growth component (Table 2). Maintenance required 59, 77, 56 and 56% of the total energetic needs for the period 15 July–15 October in the years 1985–1988. Table 3 compares the amount of fish eaten by grebes and perch for different periods throughout the season. Assuming a linear increase in the grebes' foraging range as

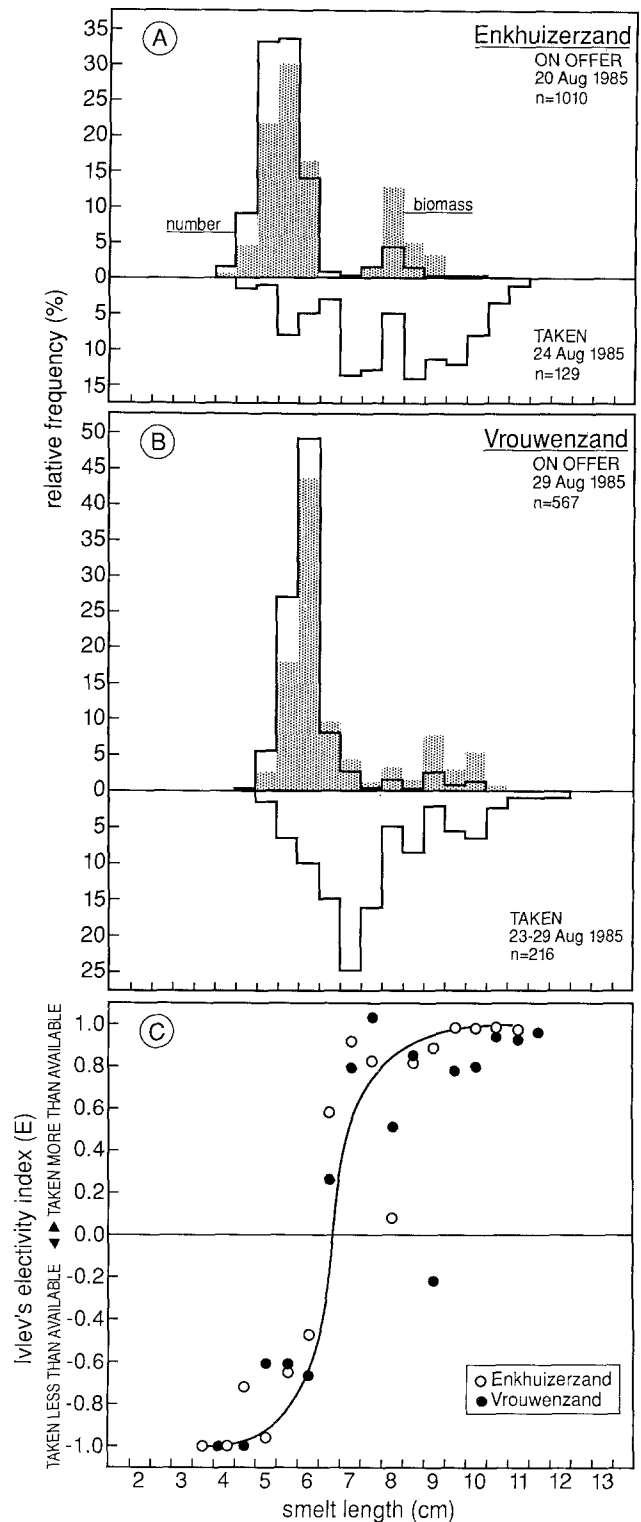


Fig. 6. Comparison of the size distribution of smelt present at Enkhuizerzand and at Vrouwenzand in Lake IJsselmeer (combining bottom and surface catches) and the size distributions of smelt ingested by great crested grebes (from otolith lengths) at these sites at exactly the same time. The size preference of grebes is summarized in panel C by Ivlev's electivity index E (Jacobs 1974), indicating a switchpoint in preference at 6.5 cm (line drawn by eye)

Table 2. Food consumption by piscivorous perch needed for maintenance and growth, expressed in kJ/ha and converted into smelt (kg/ha) using an energy content of 4.5 kJ/g and a gear efficiency of catching perch of 12.5%

	1985	1986	1987	1988
Maintenance (kJ/ha)	223 199	461 164	586 100	181 444
Growth (kJ/ha)	153 677	134 771	461 648	141 704
Total consumption (kJ/ha)	376 876	595 935	1 047 748	323 148
Smelt consumed (kg/ha)	83.7	132.4	232.8	71.8

All values refer to the Vrouwenzand area for the period 15 July–15 October

Table 3. Standing stock of smelt in the study area at Vrouwenzand at different sampling dates in 1985–1988

Date of sampling	Days per interval	Smelt stock (kg/ha)	Change biomass smelt ^a (kg/ha/day)	Cumulative predation			Predation per interval			
				Grebes (kg/ha)	Perch (kg/ha)	Total (kg/ha)	Grebes (kg/ha)	Perch (kg/ha)	Total (kg/ha)	Total (kg/ha/day)
29 Aug. 1985	14	30.1	+0.886	4.20	45.44	49.64	0.42	13.00	13.42	0.959
12 Sep. 1985	13	42.5	+0.385	4.62	58.44	63.06	1.15	10.96	12.11	0.932
25 Sep. 1985	15	47.5	+0.353	5.77	69.40	75.17	0.92	14.32	15.24	1.016
10 Oct. 1985		52.8		6.69	83.72	90.41				
23 Jul. 1986	14	32.3	-0.157	0.25	13.64	13.89	0.67	17.20	17.87	1.276
6 Aug. 1986	13	30.1	+0.031	0.92	30.84	31.76	2.40	17.64	20.04	1.542
19 Aug. 1986	16	30.5	-1.613	3.32	48.48	51.80	3.40	32.68	36.08	2.255
4 Sep. 1986	13	4.7	-0.185	6.72	81.16	87.88	2.58	20.80	23.38	1.798
17 Sep. 1986	14	2.3	+0.300	9.30	101.96	111.26	2.67	12.36	15.03	1.074
1 Oct. 1986	14	6.5	-0.129	11.97	114.32	126.29	1.56	18.08	19.64	1.403
15 Oct. 1986		4.7		13.53	132.40	145.93				
20 Aug. 1987	27	56.2	-0.948	3.15	96.00	99.15	6.93	70.00	24.43	0.905
16 Sep. 1987	30	30.6	-0.887	10.08	166.00	176.08	5.85	66.84	22.56	0.752
16 Oct. 1987		4.0		15.93	232.84	248.77				
30 Aug. 1988	36	55.2	-0.719	4.82	37.76	42.58	7.06	21.28	12.38	0.344
5 Oct. 1988	37	29.3	-0.373	11.88	59.04	70.92	2.33	12.76	5.52	0.149
11 Nov. 1988		15.5		14.21	71.80	86.01				

^a Negative values indicate decreases, positive values increases of the smelt stocks

Predation pressure of grebes and perch are presented both cumulatively and per interval. The daily fish requirement of grebes is fixed at 85 g/bird/day, while for perch both food for maintenance and growth have been taken into account as outlined in the text. All estimates for predation on smelt are expressed in kg per ha fresh mass, using 4.5 kJ/g as the energy content. The cumulative figures refer to the period 15 July–15 October with extrapolations made to compute the first period in 1985, 1987 and 1988.

outlined above, the data were transformed into kg/ha eaten. The total amount of smelt consumed by the grebes varied between 99 300 kg (1985) and 210 000 kg (1986). For 1985–1988 these values correspond to maximum consumption estimates of 0.09, 0.21, 0.26 and 0.20 kg/ha per day.

The estimated maximum consumption of smelt by perch for 1985–1988 was 0.95, 2.04, 2.59 and 0.59 kg/ha per day. Thus the predation pressure by perch exceeded that by the grebes by a factor of 2–10. Cumulatively over the period 15 July–15 October the grebes took 6.69 kg/ha in 1985 up to 15.93 kg/ha in 1987. For perch these figures were 71.80 kg/ha in 1988 up to 232.84 kg/ha in 1987.

For 1986 (the year for which we have the most detailed fishery data), smelt stock data in the course of the season (Fig. 7B) were plotted together with the total number of grebes on the roost (Fig. 7A) as well as the number of grebes actually fishing in the area where the fishing transects occurred (Fig. 7C). A large drop in smelt stocks from 30.5 to 4.7 kg/ha occurred between 19 August and 4 September. This drop cannot be explained by predation alone. The grebes' reaction to it was noticeable as a dramatic fall in overall bird numbers: from 15 000 to 8 000 within 1 week. It is likely that some of the flightless grebes

moved away to other sections of the coast. Total numbers varied considerably in the last days of August and the first half of September. From then on the grebes had to forage south of the area of our fishing transects (judged from arrival times, see Fig. 3 and confirmed by radar observations on 16/17 September). From these data we conclude that under the observed conditions of low water transparency (40 cm Secchi depth), moulting grebes accept a lower threshold level of overall smelt biomass of about 30 kg/ha. In three out of four years the stocks fell below this value at the end of the season (Fig. 1).

The reaction of grebes to the change in availability of large smelt is less clearcut. In the study area the collapse of the smelt stocks in late August was preceded by the disappearance of the 1+ cohort 2 weeks earlier (Fig. 7B). Grebes left the area when the available fraction (smelt > 6.5 cm long) fell below 7.5 kg/ha. Although the growth of the 0+ cohort from late August onwards led subsequently to a higher availability of smelt, the grebes kept foraging outside the area of our fishing transects, where biomass stayed below the threshold level. For the part of Vrouwenzand further than 5 km from the roost, the grebes apparently had better feeding conditions from late September onwards (Fig. 7A).

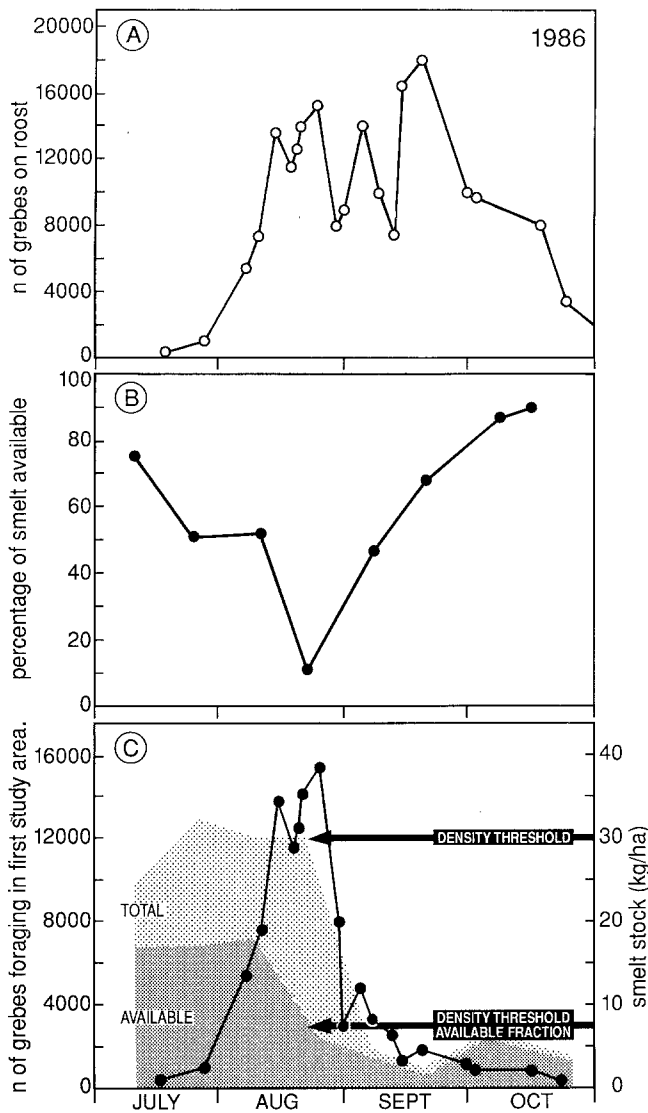


Fig. 7A. Number of grebes on the Vrouwevand roost in the course of the 1986-season, **B** The proportion of smelt available, i.e. larger than the size threshold of 6.5 cm. Prey availability shows a dip because of the disappearance of the 1+ cohort and a delay in the arrival of 0+ smelt > 6.5 cm. **C** Seasonal changes in smelt stocks in the Vrouwevand area are presented as total biomass and as "available" smelt > 6.5 cm. The drop in bird numbers foraging within the area of fishing transects followed the collapse in smelt stocks shortly after 19 August

In 1985 both predatory fish and birds were relatively scarce; in 1988 stocks of predatory perch were low compared to other years. It is striking that the lower predation pressure on smelt in 1985 and 1988 indeed appears to be reflected by the higher level of the standing stock remaining at the end of the season, compared to the same period in 1986 and 1987 (Fig. 1, Table 3).

Can these data on the impact of two different predators explain the overall pattern of smelt abundance in different years? In Fig. 8 fishing data from three of the four years are plotted against the estimated predation by grebes and perch per inter-catch interval. The data for 1988 are left out, since the intervals between catches are so large (see Table 3). Figure 8 shows that there is a significant correla-

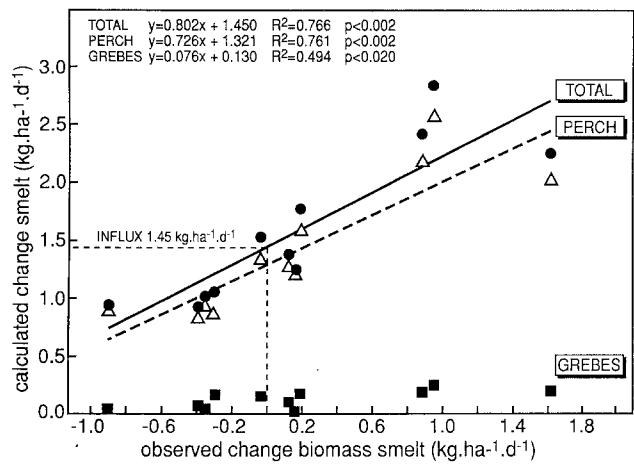


Fig. 8. Calculated changes of smelt stocks due to the combined effect of predation by perch and grebes in relation to the observed changes in smelt stocks in the Vrouwevand area. Data from 1985, 1986 and 1987. The intercept of the linear regression equation ($r^2=0.766$, $P<0.002$) suggests a continuous influx of smelt of 1.45 kg/ha per day

tion between observed and calculated change in biomass of smelt stocks due to the combined predation by fish and birds ($r^2=0.766$, $P<0.002$). This correlation is almost entirely due to the effect of predation by perch alone ($r^2=0.761$, $P<0.002$). Predation by grebes alone has a significant but less pronounced effect ($r^2=0.494$, $P<0.02$). From the intercept of the regression we estimate average immigration of smelt into the area as 1.45 kg/ha per day. This influx permitted perch to continue predation during periods of low smelt stocks, e.g. after 4 September 1986, when perch took about 51 kg/ha until mid-October, although the smelt stock present never exceeded 5 kg/ha after 4 September (Fig. 5).

Discussion

Estimating fish stocks

Measuring absolute fish densities is difficult. Studies which relate trawl-type sampling to absolute fish densities are rare and the results are highly variable (Pope et al. 1975; Dahm et al. 1992). Our fishery data can be regarded as point estimates, comparable to each other in terms of catch per unit effort (Bayley 1985). The sonar recordings showed that fish were regularly distributed and therefore the problem of the possible high contribution of schooling behaviour to the sample variance does not apply. Low water transparency, as in Lake IJsselmeer, is known to increase the catching efficiency of the trawl (Buijse et al. 1992). Our data were all gathered at the time of peak biomass of blue-green algae, so transparency was fairly constant.

Using a comparable but smaller trawl, Kuipers (1975) found an overall gear efficiency of 20% when sampling flatfish in the turbid Wadden Sea. The study by Doornbos and Twisk (1987) on the efficiency of a 3-m beam trawl for catching epibenthic gobiid fishes in Lake Grevelingen,

gave size-dependent gear efficiencies of 55–85% (30–70 mm fish length). Our 90% gear efficiency for smelt is based on sonar records run simultaneously when trawling. The towing speed of 5 km/h is much higher than the maximal sustainable swimming speed of a fish of that size (0.5–1.2 km/h; Jens 1982; Turnpenny and Bamber 1983). Fish do escape from the net, however, both by moving out of the catching area as well as due to disturbance by the ship's engine (cf. Kuipers 1975). For the larger perch we calculated a much lower, 10–15% gear efficiency. The swimming speed of this species (15–35 cm total length) is still not greater than the towing speed of our gear (Beamish 1970; Jens 1982). It seems likely, however, that the chance of escaping the 1.2-m wide mouth of the net is proportional to the swimming performance of the fish. According to the estimated endurance times for smelt the distance travelled at maximum speed would be only 0.3 m whereas the larger perch would cover at least 2.4 m. Our assumption on gear efficiency for perch probably will still lead to an underestimation of the impact of predatory perch. Although the absolute figures on predation pressure are therefore to be considered with some caution, the conclusion that the impact of predatory fish on the smelt population far exceeds that of grebes remains unaffected.

Is prey availability limiting daily food intake by grebes?

The daily food requirement of the birds can be estimated as follows. During August–October, the average body mass of both adult and juveniles is 1100 g (Piersma 1988c). Following Nagy's (1987) predictive equation of field metabolic rate of "seabirds" from body mass, each grebe would require 1110 kJ per day. Given an assimilation efficiency of 85% when feeding on smelt (balance study on captive grebe) and an energetic value of smelt of 4.5 kJ/g fresh mass, this leads to a calculated intake requirement of $1110/(4.5 \times 0.85) = 290$ g smelt per day. Obviously much less is taken according to Piersma's (1988b) estimate of 70–90 g for grebes during wing-moult. However, this can not be interpreted as the result of the food constraint only. During summer solar radiation and high water temperatures (max. c. 20°C) will reduce thermostatic costs of the grebes which leads to a saving of about two-thirds of the daily energy expenditure compared to the winter situation (J. de Vries and M.R. van Eerden in prep.). Therefore the limited food availability will hardly account for the observed reduction of total food intake per day. This conclusion is supported by the observation that during wing-moult great crested grebes do not rely on the use of any fat reserves at all (Piersma 1988b). Instead we suggest that given the reduction of thermostatic costs, the grebes can cope with the strong constraints on food availability.

Prey size selection by grebes

According to Ware (1973) the underwater sight range of a visual predator can be interpreted from an ecological viewpoint as a cognitive process involving prey size, inherent contrast and ambient illumination. Due to the

dense blooms of the blue-green algae *Oscillatoria aghardii*, *Microcystis aeruginosa* or *Aphanizomenon flos-aquae*, underwater light conditions during late summer are generally poor (Berger and Sweers 1988; Piersma et al. 1988). Moreover, because of the behaviour of the smelt the grebes are very limited in the time available for exploitation of the fish stocks. Only the periods of twilight at dawn and at dusk allow the birds to hunt the fish, which are only then present in the uppermost and most transparent water layers (Piersma et al. 1988). Grebes selected smelt larger than 6.5 cm (Fig. 6). At first sight it may come as a surprise that birds which are time-constrained should show such a high selection for the larger size classes of the smelt, especially in view of the fact that generally the larger smelt occur lower in the water layer and are thus less visible than the smaller ones (unpubl. data). There are three possible explanations of the pattern of fish size ingested: (1) active selection of the larger smelt (cf. Sjöberg 1988), (2) passive selection by size-dependent detectability and (3) passive selection by size-dependent differences in timing of upward migration.

On 29 August 1985 the stock of fish above the apparent size threshold amounted to 7.8 kg/ha out of a total stock of 30.1 kg/ha (Table 3). Selecting smelt around a mode of 7 cm (fresh mass 1.51 g) instead of the 6 cm (0.91 g) of the population mean (Fig. 6) would require 56 instead of 93 fishes to meet the daily requirement of 85 g. Given the limited time available for foraging it might seem beneficial for a grebe to ignore the smaller smelt encountered in a given dive and wait for a larger smelt to turn up. However it can easily be seen that the lower encounter rate is not compensated for by the higher prey mass. Active selection for larger prey therefore seems unlikely.

Could detectability of fish then be largely size-dependent? Support for this hypothesis is provided by the size-selection pattern of moulting grebes on the southern part of Lake IJsselmeer. Through its high silt content this part (Enkhuizerzand) has an even lower transparency than Vrouwenzand (Secchi disc values in August of 20–50 cm instead of 40–80 cm). As predicted if detectability were size-dependent the grebes indeed took the largest smelt at Enkhuizerzand (Fig. 6) despite the fact that the smelt available were smaller.

The third possibility is that the vertical migration of smelt is size-dependent. As stated by Clark and Levy (1988), planktivorous fish may move upward in search for prey at light levels high enough for them to forage at maximum rates, but too low for hunting by predators. Because of the limited time available to these fish to exploit zooplankton in the 'anti-predation window', the larger fish with higher energy demands will tend to arrive earlier in the top water layers. The grebes which are present in good time to take their share would thus meet the larger size classes first.

We are as yet unable to distinguish between the hypotheses of greater detectability or differential migration. Whatever the proximate factor causing it, the effect is clearly size-dependent predation pressure. Although the grebes did not exert such a high demand on the stocks of smelt as perch, the disappearance of the 1+ cohort in the course of the summer (Fig. 5) can mainly be attributed to avian predation.

Smelt stocks, predation rates and bird numbers

The existence of lower acceptance thresholds in fish-prey density and size for grebes may occur because of conditions of poor visibility. Blooms of blue-green algae are typical of eutrophic lakes during late summer (Sommer 1989). Was the total number of grebes on the moulting site influenced by the overall underwater visibility conditions?

In 1985 the number of grebes remained well below that in other years (Fig. 1). In that year local perch predation was low and as a consequence smelt stocks were high in comparison with other years (Table 3). However, as shown in Table 4, extremely low visibility conditions occurred that season. The data suggest that a cut-off point for grebes might exist at 40 cm Secchi depth. Of course both food density and visibility determine prey availability. As prey density decreases the grebes would require a greater visibility, thus causing a downward shift in the lower acceptable limit of Secchi depth (Eriksson 1985).

Few data exist about the actual predation rates of fish-eating birds under natural circumstances. Doornbos (1984) estimated that over a winter season in the (clear) saltwater Lake Grevelingen, great crested grebes and red-breasted mergansers *Mergus serrator* were able to consume 28–36% of the standing stock in late summer of Gobiidae, *Clupea harengus* and *Sprattus sprattus*. Over 5 months this equals a predation rate of 0.2% per day. For wing-moulting black-necked grebes *Podiceps nigricollis* preying on brine shrimps *Artemisia monica*, Cooper et al. (1984) estimated an overall predation rate of 4.3% per day. Even during the period of twilight the majority of smelt stays in the dark, i.e. below the level of 1% light at the surface. If we extrapolate echo density from the sonar recordings to the uppermost 50 cm water layer, the available fraction of total biomass over the visible part of the water column would be 20% at maximum. Thus during the periods of twilight not more than c. 6 kg/ha (1987: 11 kg/ha) would potentially be within reach. Taking into account the size threshold, however, this figure drops to c. 3 kg/ha on average. Compared to the grebes' daily removal of 0.03–0.26 kg/ha per day this would equal a 1.5–5.8% daily predation rate on the smelt really available for grebes (Table 5). These figures are higher than those found by the studies listed before. The range of our data for different intervals and different years is surprisingly constant; only in late summer 1986 did higher levels occur (31.3–45.5%). Interestingly, the latter values coincide with the sudden drop in bird numbers (Fig. 7). The constancy of these seemingly low rates probably indicates some balance between the fish available and the birds' dispersion over the

Table 4. Secchi disc values (in cm; WORSRO database) of the study area at Vrouwenzand in Lake IJsselmeer between 1 July and 15 October for the years of study

	1985	1986	1987	1988
Average	36.5	55.5	43.7	52.3
Standard deviation	12.3	11.9	16.4	15.1
<i>n</i>	10	10	12	13
Minimum	20	30	30	35
Maximum	60	70	75	85

Table 5. Predation rates by grebes on available smelt stocks

Period	Predation (kg/ha/day)	Stock available (kg/ha)	Predation rate (% taken per day)
1985			
29 Aug.–12 Sep.	0.03	1.57	1.91
12 Sep.–25 Sep.	0.09	2.38	3.78
1986			
23 Jul.–6 Aug.	0.05	3.29	1.52
6 Aug.–19 Aug.	0.18	3.13	5.75
19 Aug.–4 Sep.	0.21	0.67	31.34 ^a
4 Sep.–17 Sep.	0.20	0.44	45.45 ^a
1987			
20 Aug.–16 Sep.	0.26	9.10	2.86

^a Strong decline in grebe numbers

Smelt availability is set by the degree of upward migration (maximally 20% of total stock) and fish size (only smelt > 6.5 cm). Only periods when grebes actually foraged within the sampling area of the fish were taken into account

feeding areas, reaching maximum densities of 1–3 birds/ha. Disturbance by only a few hunting grebes may push the smelt back into deeper water. Field data or trials with captive birds under semi-natural circumstances combining prey availability, predation rates and foraging success are needed to check the minimum fish density necessary for grebes to forage efficiently.

Exploitation of smelt stocks: competition or facilitation between predatory fish and birds?

The continuous immigration of smelt into the area allows both perch and grebes to use the Vrouwenzand area for a few months. Predatory fish consume smelt at a rate up to 10 times that of the birds. Although perch (15–35 cm) preyed on average on much smaller smelt than grebes did, they are in direct competition. Due to the fast growth rate of smelt the consumption of juvenile smelt by perch implies a reduction of the potential stocks becoming available to the grebes later in the season.

On the other hand pursuing perch might move the smelt to the upper water layers where they could be hunted by the grebes. This phenomenon of facilitation has been described in ocean waters where tuna and also cetaceans enhance predation by birds in the top layer (e.g. Safina and Burger 1985; Camphuysen and Den Ouden 1988). Perch is known to be a day-active species (see Müller 1978 for review) with marked locomotor activity at dawn and dusk in clear waters (Alabaster and Stott 1978; Reynolds and Casterlin 1979). However, Craig (1977, 1978, 1987) reported extended activity throughout the day at times of low visibility due to algal blooms. In the turbid Lake IJsselmeer the daily pattern of hunting activity by perch has not been studied but is probably not unlike the situation described by Craig for Windermere. This pattern would differ from that of the grebes which are only active at dawn and at dusk, which makes facilitation rather unlikely. Rather, perch seems to be a more efficient predator at low light levels and the competitive relationship with grebes is far more important.

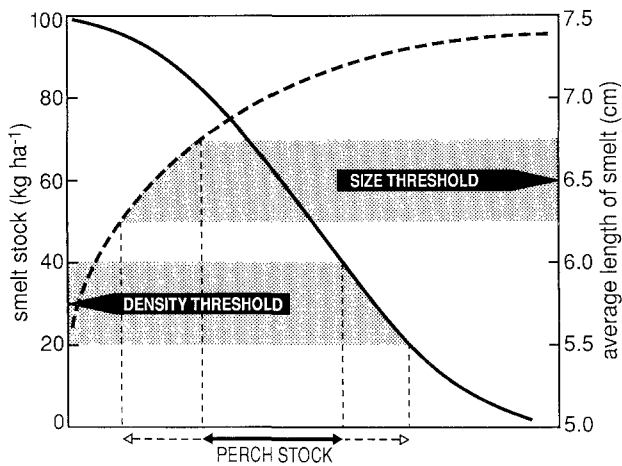


Fig. 9. Conceptual model describing the effect of predation by perch on smelt in relation to food availability for grebes. Competition between perch and grebes would occur at moderate or high levels of biomass of the predatory fish causing a reduction of smelt biomass (*density threshold* for grebes indicated). At low levels of perch, the increased smelt population would again reduce foraging abilities of the grebes because of a reduction in growth rate of the planktivorous 0+ smelt by intraspecific competition (*size threshold* for grebes indicated). The two thresholds (indicated as ranges rather than fixed values) would imply an optimum predator fish density to allow simultaneous predation by grebes as well

Implications of competitive interactions between birds and predatory fish

Predatory fish have an important effect on prey availability. Over the 4 years of study, the fish predators in the study area took 90% of the smelt consumed by grebes and perch together. Given the high demands on fish density and fish size by the avian predators, their vulnerable position in competition with predatory fish is obvious. When the latter are abundant this causes a reduction of the total stock available. However, as a result of predation, the remaining smelt may become larger as a result of reduced competition with conspecifics (Weatherley 1972; Abrosov and Agopov 1957; Lillielund 1961). This in turn would favour the grebes. Both effects, which depend on the existence of density and size threshold values, suggest that there should be an optimal density of predatory fish for the site to serve as moulting area for great crested grebes (Fig. 9). The current over-exploitation of the stocks of predatory fish by commercial fisheries (Buijse et al. 1990; Dekker 1991) therefore is likely to have had a positive effect on food availability for grebes. In a situation without fisheries the stock of 0+ perch and pikeperch would be larger, and they might provide an alternative food source. However, the fact that these species are less dependent on zooplankton for their food (Buijse 1992), means that they less often occur in the uppermost water layers, thus staying out of reach of the grebes (Piersma et al. 1988). We therefore hypothesize that, given the poor visibility conditions caused by the eutrophic state of the lake, only the artificial lessening of competition between birds and predatory fish due to human over-exploitation of the latter allows the avian predators to exploit the rich food source provided by the pelagic smelt.

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