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Food of roach (*Rutilus rutilus*) and ide (*Leusiscus idus*): significance of diet shift for interspecific competition in omnivorous fishes

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Summary. Feeding relationships between roach and ide from two sites in a mesotrophic lake SE Norway are presented and discussed. When animal food supply was scarce, both fish species increased their consumption of macrophytes; roach sevenfold, and ide threefold. Along a typical littoral vegetation gradient, ide fed among helophytes, while roach fed in the zone outside. This different habitat selection was reflected in the most important plants consumed (ide: *Equisetum fluviatile,* roach: Characeae), and confirmed by gill net catches. During the vegetative season, roach avoided areas with dense vegetation. In shallow areas beyond the littoral, the most important food plant for both fish species was *Potamogeton perfoliatus,* which constituted 80% of the total food consumed (dry weight basis) in the roach and 35% in the ide. The diet shift to plants seemed to be strongly influenced by the supply of animal food and the intensity of intra- and interspecific competition.

Being an almost "perfect" generalist in food preference, with a broad food spectrum and at the same time having the ability to survive on very few food items, roach frequently dominate fish communities in mesotrophic and eutrophic lakes. Many authors consider that mesotrophic and eutrophic lakes with littoral vegetation favour its presence (Hartley 1947; Svärdson 1975; Prejs 1978). Participating in internal nutrient cycles (Andersson et al. 1978; Brabrand et al. 1984), structuring lake zooplankton (Stenson 1975; Svärdson 1975) and being prey for predatory fishes, roach is an important component in lake metabolism.

In contrast to roach, ide rarely dominates fish communities, although this species is usually found together with other cyprinids. Like roach, ide has a varied diet, generally planktivorous as a juvenile, but changing to plants, benthic animals and fish as an adult (Cala 1970).

The aim of the present study is to document the diet of roach and ide in two environments with differing fish communities as well as different aquatic plants and available prey species. Special attention is given to the consumption of plants, and the feeding habitat selection of the two species in relation to the plant community. Diet shift to low energy food in omnivorous fishes from animal food to plants, detritus or even sediments seems to be influenced by intra- and interspecific competition (Mann 1965; Lessmark 1983; Persson 1983). The potential to change in diet reduces competition for food in periods when animal food supply is scarce, thus permitting the maintainance of high fish densites. The feeding patterns present in the two environments provide the opportunity to discuss the feeding of roach and ide in the presence and absence of strong competition from bottom feeding fishes such as bream and white bream.

Study area

Lake Øyeren is part of the Glomma river system (Fig. 1). Fish for this study were collected from two areas, both situated in the northern delta area, formed by the inflowing rivers Glomma, Leira and Nitelva.

The whole of Lake Øyeren has 23 fish species, nearly all of which inhabit the deeper part of the main lake basin during winter. Migration into the shallow delta area occurs which raising water levels and temperatures in May/June.

Station A. Secci disc transparency during summer was about 0.5 m, and water depth 2.5–3.0 m. The plant com-

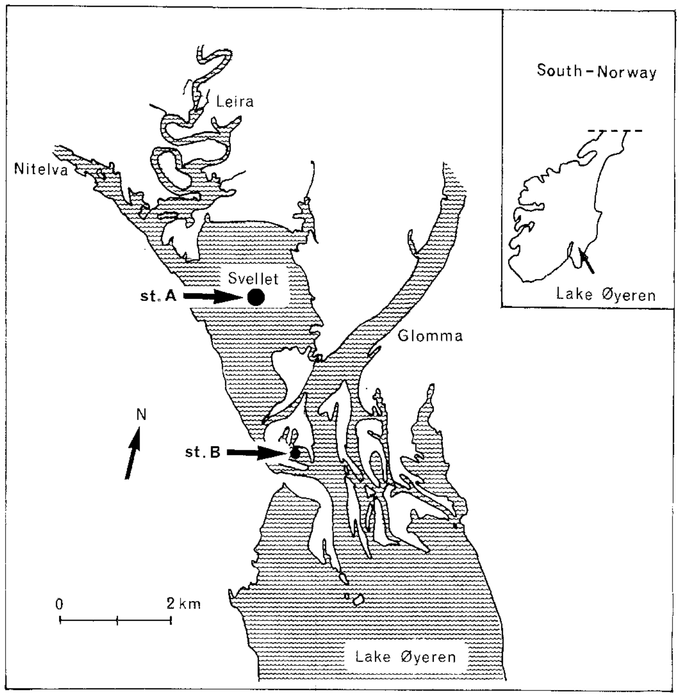

Fig. 1. Northern part of Lake Øyeren. Fishing sites are indicated

munity was dominated by circular colonies of *Potamogeton perfoliatus*. In the middle of June, the colonies were only 1–3 m in diameter and widely separated (ca. 100–500 m). The colonies subsequently increased in diametre until they more or less merged into each other before they disappeared in October.

Apart from the macrophytes, available food items for fish were dominated by the cladoceran *Sida crystallina* and *Bosmina longirostris* and for bottom feeding fishes by zoo-microbenthos living on the sediment surface (Brabrand 1984). Macroinvertebrates were almost absent, probably due to annual drying out of the area and heavy fish predation.

Gill net catches (mesh size: 24, 29, 35, and 45 mm) in the northern shallow part at st. A were by numbers dominated by roach (42%), bream (12%) and white bream (8%), while perch, bleak, dace, chub, ide, asp, pike, ruffe and pike-perch occurred regularly in small numbers (Hansen 1978). However, recent investigations by Backe-Hansen (1982) using other methods indicate that bleak and ruffe are more numerous in this area.

Station B. Secci disc transparency usually exceeded maximum depth (2 m), and littoral and sublittoral plant communities were well developed. The vegetation belt showed the general zonation from terrestrial to aquatic environments (*Carex, Equisetum* and *Isoetes* zone). From about 0.2–1.2 m the waters were dominated by *Equisetum fluviatile* with some small areas of *Utricularia vulgaris, Sagittaria sagittifolia* and *Drepanocladus.* Outside the helophytes, species of Characeae, mainly *Chara braunii* dominated in spring and in summer until August, with small spots of *Isoetes echinospora, Potamogeton pusillus* and *Eleocharis acicularis.* From August until October, this zone was almost totally occupied by *Myriophyllum alterniflorum, Ranuculus peltatus,* and to some extent *Potamogeton perfoliatus.*

In contrast to st. A, the animal food supply for fish was dominated by macroinvertebrates (Mollusca, Trichoptera, Coleoptera, Ephemeroptera, *Asellus aquaticus*) and Cladocera.

Gill net catches were dominated by roach (81%), with perch and ide constituting 8% and 6% respectively. Bream and white bream were nearly absent.

Materials and methods

Roach and ide were collected from May 1974 to June 1975 from st. A, except during the period with ice cover (Oct.–Apr.). Fish from st. B were collected from May 1974 to October 1975. Sets of gill nets with mesh sizes 24, 29, 35 and 45 mm were used twice a month. From both sites, up to 40 specimens of each species were examined each month. The total number of examined roach were: st. A: 357, st. B: 504, and of ide; st. A: 164, st. B: 262. During the period of ice cover at st. B (Dec.–Apr.), a total number of 44 roach and 22 ide were examined.

Following capture, the fish were measured, weighed, sexed and the alimentary tract removed. The gut contents as far back as the point of entry of the bile duct were removed. No difference in fish length distribution within each species (roach: 14–32 cm, ide: 18–50 cm) was observed between the two sites.

Gut contents were analyzed according to Ricker (1968). Dry weights of ingested animals were estimated using the regression function for the length-weight relationships of prey animals collected from the lake. No significant difference in size between consumed animals and animals collected from the lake was found (Students's *t*-test, $P > 0.05$). Larvae of chironomids from the gut were measured directly and their weight determined by the length-weight regression equation $\log l = 3.22 \log W + 3.41 \cdot 10^{-4}$ ($r = 0.93$, l = body length in mm, W = dry weight in mg). Plants were sorted into dead (detritus-like) and living (with chlorophyll) plants, the latter being determined taxonomically. The groups of plants were dried and weighed separately. The dry weight of *Equisetum fluviatile* was corrected due to a significant weight decrease of 3.3% ($P < 0.05$) after storage in ethanol.

Dietary resemblance between the fish species can be expressed by Sorygin's index (Sorygin 1939), based on weights of the prey groups present in the guts. A high value indicates a high degree of similarity.

Habitat selection of roach and ide was examined by comparison of gill net catches in the helophyte and submerged vegetation zones from June to October 1975 at st. B. In both vegetation zones, three gill nets of each mesh size (24, 29, 35 and 45 mm) were used. Fishing was carried out during 10 hours at night. The difference in number of each species was tested (Students' *t*-test), assuming that the catchability of each species was similar in the two zones.

Results

Gut contents

Station A. At st. A macrophytes constituted on average about 80% of total dry weight of gut contents of roach throughout the study period, while the remaining 20% was animal material and detritus (Fig. 2). Macrophyte grazing started in June or July and continued until September, reflecting the period during which living plant material was available. Feeding maximum was observed in September, with a mean gut content of 33.9 mg dry weight, of which 32.1 mg was living plant material.

In the gut contents of ide 35% of the total gut contents was macrophytes. Grazing started in June during 1974 and in May during 1975 (Fig. 2). In both fish species, *Potamogeton perfoliatus* dominated, although *Equisetum fluviatile* was present in variable amounts in the ide (Fig. 4). Ide fed mainly on young shoots of *P. perfoliatus,* while mature leaves dominated in the gut contents of roach.

Animal material was in general found in only a few individuals of both fish species, and was only of importance before and after the period during which *P. perfoliatus* was available (Fig. 2). Chironomids were present in frequencies up to a maximum of 55%. The bryozoan, *Plumatella fungosa,* was eaten by both species in August and September when the colonies were well developed. Fish eggs were observed in the gut of both species in May and fish fry (Cyprinidae 0+, 1+) during the autumn.

Station B. At st. B, living plants constituted 28% of total gut contents of roach, but only 5% in ide (Fig. 3). Plant material in roach was clearly dominated by Characeae (Fig. 5). Three species were recorded with *Chara braunii* dominating, while *Nitella mucronata* and *N. opaca* were recorded in smaller amounts. Ide fed almost exclusively on *E. fluviatile* (Fig. 5). Filamentous algae (*Zygnema* sp. and

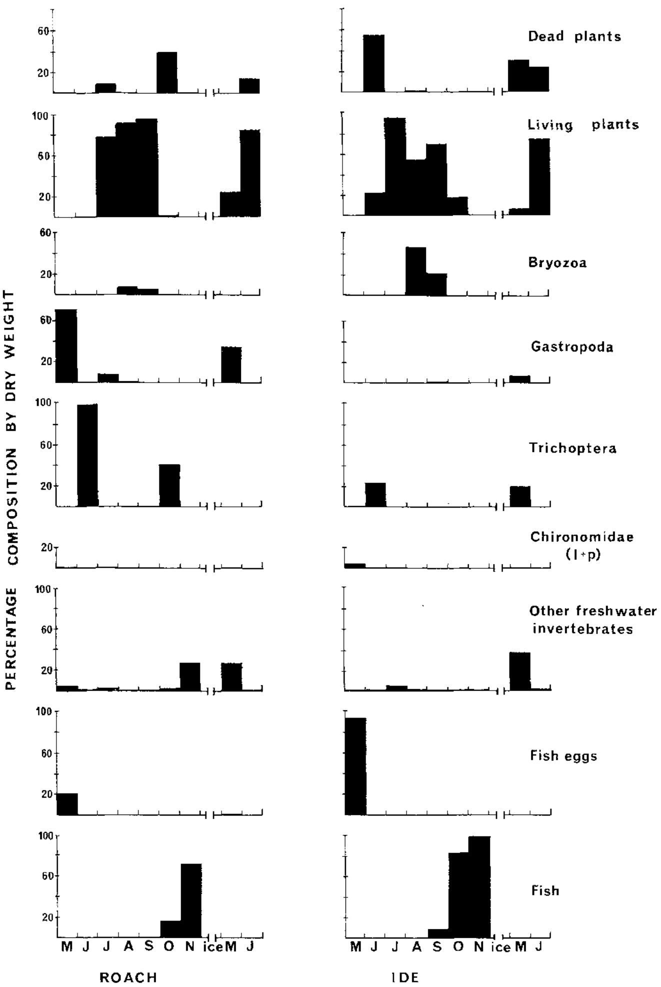

Fig. 2. Percentage composition by dry weight of gut contents of roach and ide collected from st. A in Lake Øyeren

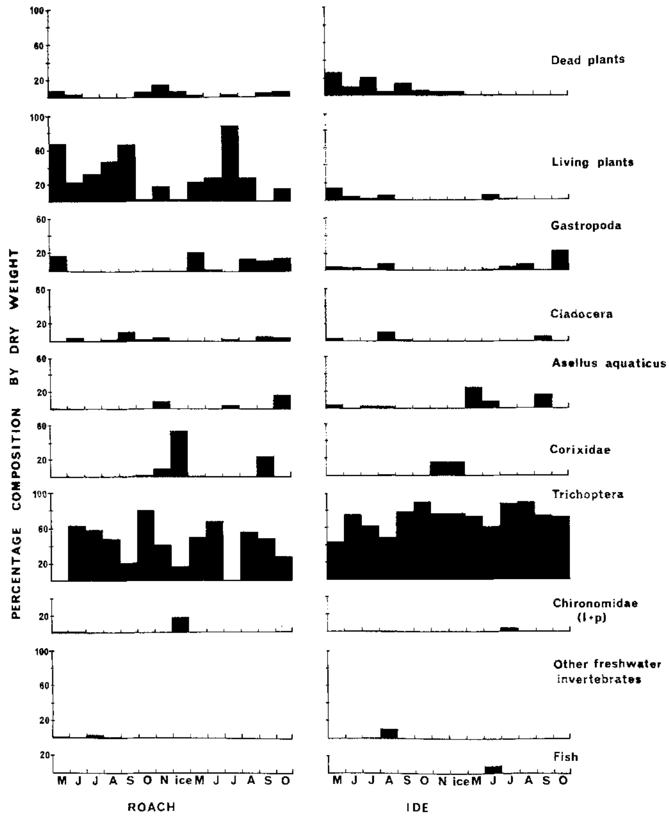

Fig. 3. Percentage composition by dry weight of gut contents of roach and ide collected from st. B in Lake Øyeren

Mougeotia sp.), mosses (*Drepanocladus* sp.), *Potamogeton* (*P. pusillus* and *P. obtusifolius*) and *Myriophyllum alterniflorum* were all observed in greater amounts in roach than in ide.

The animal food items at st. B were usually dominated by larvae of Phryganidae (Trichoptera), which constituted 20–80% of the dry weight of the gut contents of both fish species (Fig. 3). In roach *Oxyethira* was also found, but it never exceeded 2.6% of total gut contents, due to its small size. Other insect larvae, Mollusca and *Asellus aquaticus* were all observed in higher frequencies (% occurrence) in ide than in roach, while on dry weight basis the picture was less clear. Only one specimen of ide was found with fry in its gut.

Eurycercus lamellatus was the most important cladoceran for both species (Fig. 6). It had a single maximum in ide in both years, while two peaks were observed in roach, first a relatively small one in early summer and then the maximum in September. In both species the peaks in 1975 were lower than in 1974. Other cladoceran were observed in high frequencies, but in contrast to *E. lamellatus*, they always constituted less than 1.0% of total gut contents (dry weight) (Fig. 7). In roach, *Ophryoxus gracilis* dominated in summer, while *Sida crystallina* increased during autumn. Copepoda were present in spring and early summer. In the ide, *Daphnia* was more important during the summer of 1974, and small Chydoridae (mainly *Chydorus sphaericus*) during 1975.

Feeding in relation to fish length

The frequency of occurrence of the four main food categories in relation to fish size in given in Fig. 8. The general picture showed an increased frequency of plants in larger fish of both species, paralleled by a reduced frequency of zooplankton. An exception to this was the consumption of zooplankton by roach at st. A, due to the consumption of older *Potamogeton* leaves with the associated cladoceran *Alona affinis*.

Habitat segregation/food niche overlap

Net catches of ide were relatively stable both inside and outside the helophyte belt (Fig. 9) and no significant difference ($P > 0.05$) between the two habitats was observed.

Catches of roach showed no difference between these vegetation zones when the elodeids *M. alterniflorum* and *R. peltatus* dominated in August and September. In spring and late autumn when submerged vegetation was almost absent, catches of roach were significantly greater among the isoetids compared to the helophyte zone ($P < 0.05$).

At st. A, both ide and roach were closely associated with the *Potamogeton* colonies during feeding, as shown by the considerable consumption of this plant. However, as young shoots were more frequently observed in ide to-

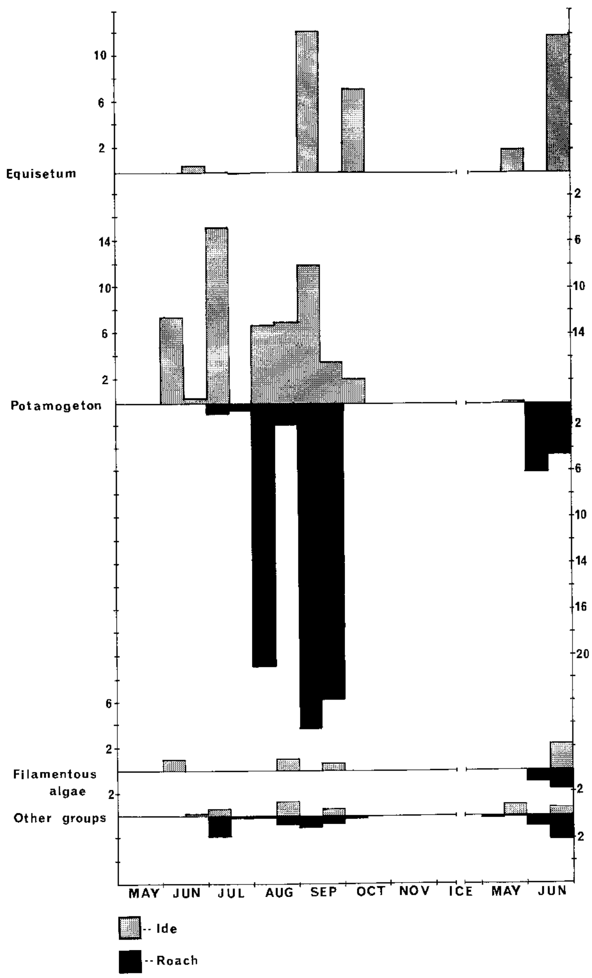

Fig. 4. Percentage composition by dry weight of total living plant material observed in the gut contents of roach and ide at st. A in Lake Øyeren

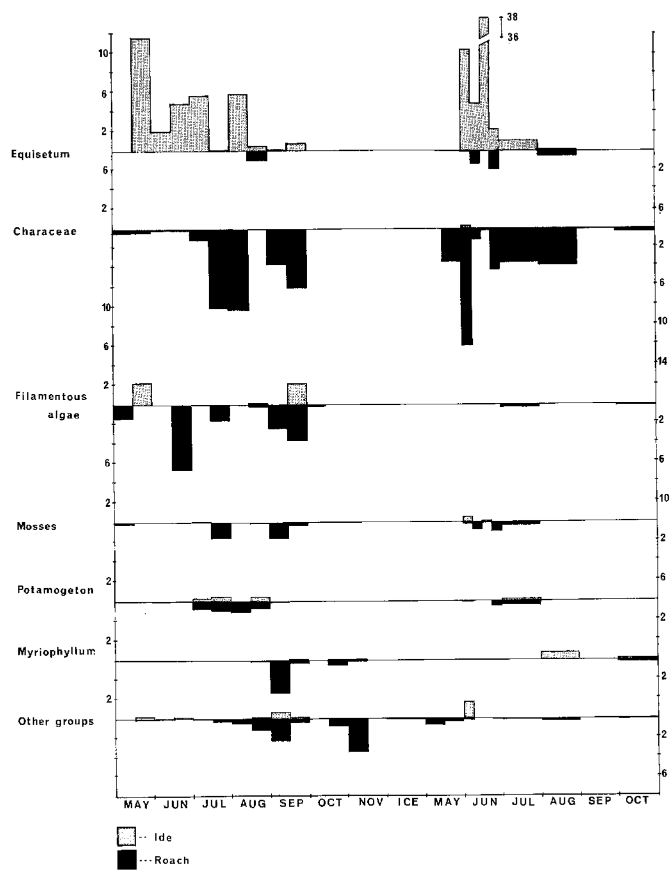

Fig. 5. Percentage composition by dry weight of total living plant material observed in the gut contents of roach and ide at st. B in Lake Øyeren

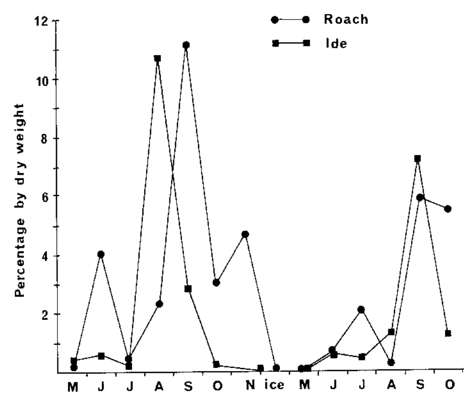

Fig. 6. Percentage of *Eurycercus lamellatus* in terms of total gut contents by dry weight in roach and ide at st. B in Lake Øyeren

gether with associated phytophile Cladocera, this indicates that the ide feed in the upper parts of the vegetation, while roach feed more on old leaves where Zoomicrobenthos as Ostracoda, *Dorylaimus stagnalis* and *Alona affinis* occur.

The index of food similarity (Sorygin's index) between the two fish species were quite similar at st. A (Fig. 10), reflecting the tendency of both species to feed on *P. perfoliatus* during the most intensive feeding period. At st. B the index showed a quite different pattern when based on plants and animal food components. The index values were in general below 20% for plants, which indicates that food niche overlap was low regarding plant consumption. Based on animal food items, the index was between 30 and 75%, except in winter when feeding in general was low.

Discussion

The dominance of plant material in the diet of roach has been shown by many authors (Kempe 1962; Hartley 1947; Mann 1965; Prejs 1978), and includes plants such as Characeae, *Elodea* and *Potamogeton*. In general, roach do not seem to be very selective in plant consumption, and the most abundant plants are those most frequently eaten. The tendency for diet shift from zooplankton and benthos to plants with increasing fish size was observed in both fish species, although in roach this seemed more obvious. Roach fry feed mainly on phytoplankton in the littoral. As juveniles they feed on zooplankton, and on all sorts of benthos, benthic algae and macrophytes when adult (Svärdson 1975). The wide range of food items reported in literature reflects the wide range of habitats occupied by roach. This also enables the roach to reduce both intra and interspecific competition to a minimum, due to the different habitat selection of the different age groups. Hartley (1947) found that zooplankton was an important food items in small roach, while Prejs (1973) observed up to 20% by weight

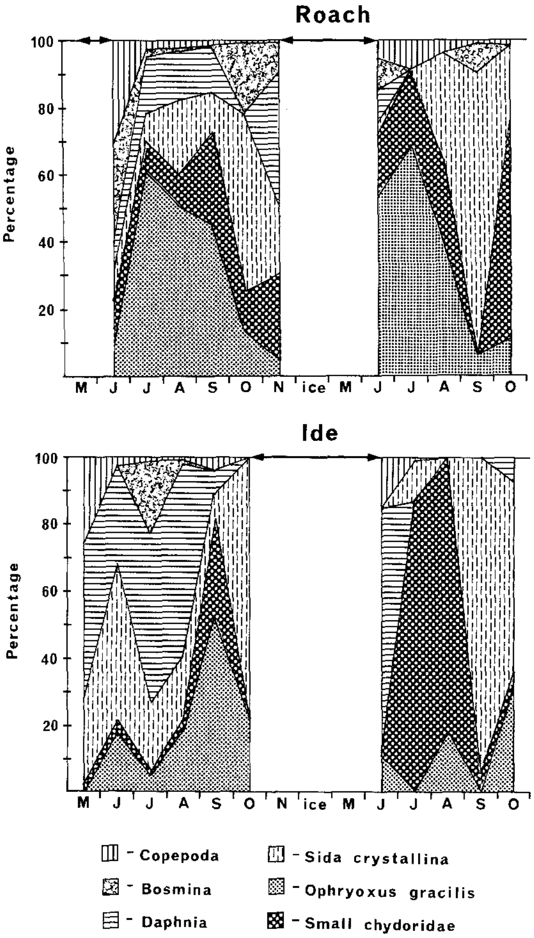

Fig. 7. Percentage composition of Cladocera (except *Eurycercus lamellatus*) by dry weight in gut contents of roach and ide at st. B in Lake Øyeren. Arrows indicate period without Cladocera in the gut contents

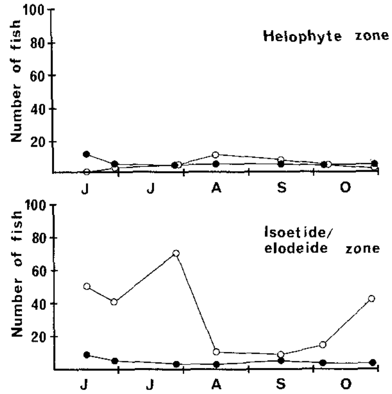

Fig. 9. Net catches of roach (open circles) and ide (filled circles) (per net length and night) in two dominant vegetation zones at st. B in Lake Øyeren

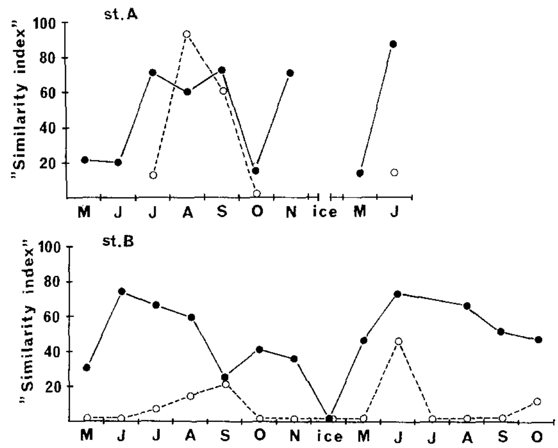

Fig. 10. Sorygin's index of food similarity between roach and ide based on living plant material (*open circles*) and animal food items (*filled circles*) at st. A and st. B in Lake Øyeren

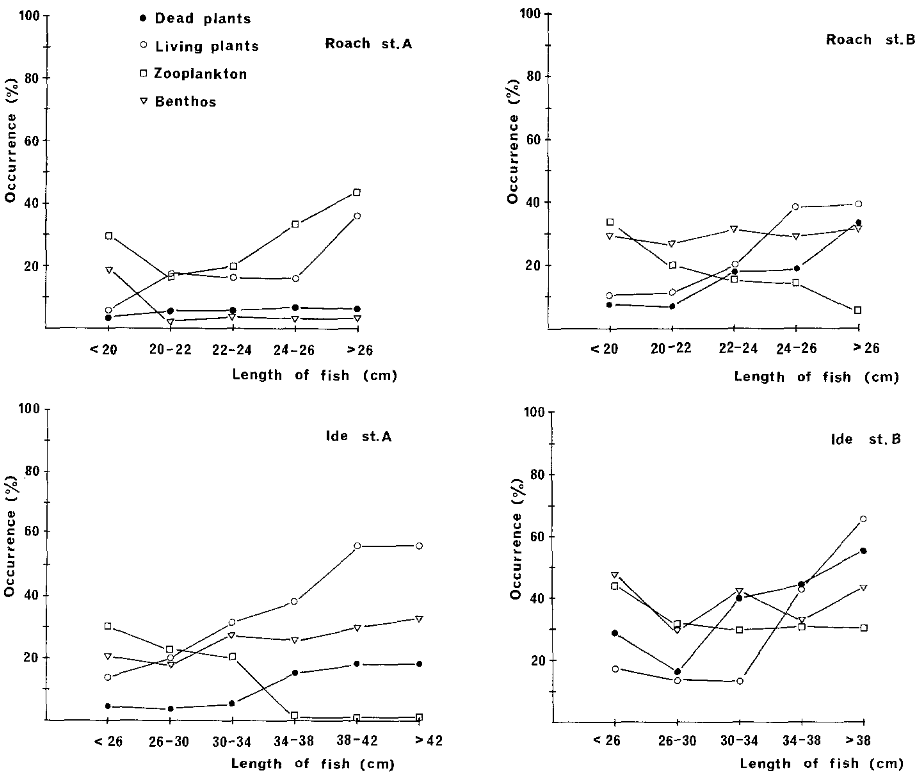

Fig. 8. Frequency of occurrence of four main categories of food in relation to body length of roach and ide at st. B in Lake Øyeren

of zooplankton in young roach. Adult roach fed almost completely on macrophytes. Cala (1970) found zooplankton to be of some importance for ide less than 20 cm. The amount of zooplankton consumed in Lake Øyeren was very low within the examined size groups in both species, probably due to high densities of fry with a high capacity to predate on zooplankton. An exception was *Eurycercus lamellatus,* which was consumed by adult roach and ide because of its larger size.

Predation on fish fry was observed in both species during autumn at st. A, probably influenced by the reduction of available zoobenthos and plants. Fry of cyprinids are closely related to the fields of *Potamogeton.* During disappearence of these fields, fish fry is easily available for predation. This is confirmed at st. B by the complete lack of fish predation in roach, and the highly reduction in the ide. The helophytes here are complete until next spring and fish fry can therefore more easily escape predation by older fish.

As ide and roach both feed on a wide range of animal food items, these components are of less importance in discussing delimited feeding habitats, compared to plants which often show a well defined zonation. Net catches at st. B showed a different habitat selection between roach and ide, which also reflects the different plants found in the gut contents of both species. These plants could only be grazed by the fish in well defined habitats, related to the different vegetation zones. Net catches showed that ide were almost evenly distributed between the helophytes and the plant community outside. Due to the very high preference for *E. fluviatile,* and the fact that animals and plants were mixed in the gut, we can conclude that ide generally fed in the helophyte zone. The preferred habitat of roach outside the heleophytes is confirmed by the high consumption of Characeae and the net catches. However, during periods with dominance of elodeids, roach seemed to avoid this zone, as in late summer and early autumn, but reinvaded this zone after the disappearence of these plants in late autumn. Similar habitat selection was observed by Prejs (1973), where roach in spring and late autumn only sporadically fed in the littoral, overgrown with vegetation. The more pelagic or semi-pelagic habit in roach is also well documented by several authors (Svärdson 1975; Eie and Borgstrøm 1978; Bohl 1980; Brabrand et al. 1984). In contrast to roach, ide show a more solitary life when adult (Cala 1970), which will provide a better opportunity for utilizing a littoral habitat among macrophytes.

The greater vertical spatial segregation between the two species at st. A was not documented by gill net catches. However, ide were not very numerous in this area, and the fact that some individuals of ide had *E. fluviatile* in their gut contents, indicates that ide were more common in littoral areas.

Conditions affecting competition were quite different at the two sites (Hansen 1978). The feeding shift in omnivorus adult fish to vegetation will reflect the availability of animal food items and the competition for food in the habitat. Both fish species showed an increased uptake of plants as the number of fish species increased and the availability of animal prey was reduced. Being omnivorous, it seems that in environments with severe food competition or low availability of animal prey, roach can obtain a large proportion of their food from sediments and plants, thus enabling them to maintain high fish densities (Mann 1965; Persson 1983; Brabrand et al. 1985). Lessmark (1983) has shown that an addition of plant food to a suboptimal ration of animal food considerably increased the growth rate of roach. This feeding strategy has high competitive value, and Lessmark (1983) believed this to be one of the most important factors for the increased dominance of roach during the process of lake eutrophication. Comparing the two sites, the consumption of plants increased in roach threefold when the supply of animal items was reduced, while in the ide a sevenfold increase was observed. However, as already shown in this research, roach also consumed many more different plants than ide (Fig. 5), demonstrating the greater omnivorous tendency in roach.

Comparing st. A and st. B, the yield of ide was nearly similar, while the yield of roach was nearly doubled at st. B when bream and white bream were nearly absent. It is interesting to note that roach, when living in the absence of bream and white bream, but in environments with strong intraspecific competition, often shows increased consumption of littoral sediments instead of macrophytes (Brabrand et al. 1984). In such lakes the role of bream and white bream, feeding almost exclusively on the bottom, is taken over by the roach, while in lakes where these species are present, omnivorus species such as roach and ide show a diet shift to vegetation. Plants, detritus and sediment components as food for omnivorous fishes have a stimulating effect on different trophic levels, due to the amount of finely desintegrated and little digested material being spread into the lake. However, as shown by different authors, the feeding on plants and detritus by fishes stimulates the decomposing food chain in general, and only in an indirect way influences primary production. When feeding on littoral sediments, roach can directly take part in the recycling of sedimented nutrients and release phosphorus, nitrogen (Brabrand et al. 1985) and iron (Brabrand et al. 1984), which is immidiately available for phytoplankton growth. Internal nutrient loading and the stimulating effect on the decomposing food chain by roach populations will thus be strongly influenced by the nature of interspecific competition for food.

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References

Andersson G, Berggren H, Cronberg C, Gelin C (1978) Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59:9–15

Backe-Hansen P (1982) Age determination, growth and maturity of the bleak *Alburnus alburnus* (L.) (Cyprinidae) in lake Øyeren, SE Norway. Fauna Norv Ser A3, 31–36

Bohl E (1980) Diel pattern of pelagic and feeding in planktivorus fish. Oecologia (Berlin) 44:368–375

Brabrand Å (1984) Microhabitat segregation between bream (*Abramis brama* (L.)) and white bream (*Blicca bjoerkna* (L.)) in a mesotrophic lake, SE norway. Pol Arch Hydrobiol 31:99–108

Brabrand Å, Faafeng BA, Källqvist T, Nilssen JP (1984) Can iron defecation from fish influence phytoplankton production and biomass in eutrophic lakes? Limnol Oceanogr 29:1330–1334

Brabrand Å, Faafeng BA, Nilsson JP (1985) Fish nutrient dynamics in a deep mesotrophic lake. Verh Internat Verein Limnol 22:2553

Cala P (1970) On the ecology of the ide Idus idus (L.) in the river Kävlingeån, south Sweden. Rep Inst Freshwat Res Drottningholm 50:45–99

Eie JA, Borgstrøm R (1978) Distribution and food of roach (*Rutilus rutilus* (L.)) and perch (*Perca fluviatilis* L.) in the eutrophic lake Årungen. Norway Verh Internat Verein Limnol 21: 1257–1263

Hansen LP (1978) Forekomst og fordeling av noen fiskearter i Nordre Øyeren. (Abundance and distribution of some fish species in northern part of lake Øyeren). Fauna 31:175–183

Hartley PHT (1947) The natural history of some British freshwater fishes. Proc Zool Soc Lond 117:129–254

Kempe O (1962) The growth of the roach (*Leuciscus rutilus* L.) in some Swedish lakes. Rep Inst Freshw Res Drottningholm 44:42–104

Lessmark O (1983) The utilization of plant material for metabolism and growth by roach (*Rutilus rutilus*). In: Competition between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in south Swedish lakes. Doctoral Dissertation, p 172

Mann KH (1965) Energy transformations by a population of fish in the river Thames. J Anim Ecol 34:253–273

Persson L (1983) Food consumption and the significance of detritus and algae to intraspecific competition in roach Rutilus rutilus in a shallow eutrophic lake. Oikos 41:118–125

Prejs A (1973) Experimentally increased fish stoch in the pond-type Lake Warniak. IV. Feeding of introduced and autochtonous non-predatory fish. Ecol Pol 21:465–505

Prejs A (1978) Lake macrophytes as the food of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophtalmus* L.) II. Daily intake of macrophyte food in relation to body size of fish. Ecol Pol 26:537–553

Ricker WE (1968) Methods for assessment of fish production in fresh waters. IBP handbook 3. Blackwell, Oxford

Sorygin AA (1939) Pitanie, izbiratel 'noja sposobnost' i pishchevye vzaimootnoshenija nekotorykh Gobiidae Kaspijskogo morja. (Foods and food preference of some Gobiidae of the Caspian sea). Zool Zh 18:27–53

Stenson J (1975) Fish predation effects on the species composition of the zooplankton community in eight small forest lakes. Rep Inst Freshwat Res Drottningholm 52:132–147

Svärdson G (1975) Interspecific population dominance in fish communities of Scandinavian lakes. Rep Inst Freshwat Res Drottningholm 55:144–171

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