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FEEDING BEHAVIOUR AND HABITAT SHIFT IN ALLOPATRIC AND SYMPATRIC POPULATIONS OF BROWN TROUT (SALMO TRUTTA L.): EFFECTS OF WATER LEVEL FLUCTUATIONS VERSUS INTERSPECIFIC COMPETITION.

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ZOOLOGISK MUSEUM

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Forord

Laboratorium for ferskvannsøkologi og innlandsfiske ved Universitetet i Oslo har ønsket å utnytte tidligere innsamlet materiale ved reguleringsundersøkelser i en regional undersøkelse. Hensikten har vært å øke kunnskapen om virkning av vassdragsreguleringer på fisk og næringsdyr. Det er fra Vassdragsregulantenes Forening (VR) bevilget forskningsmidler som har muliggjort sammenstilling av resultater om næringsvalg for ørret.

Den foreliggende rapport omhandler næringsvalg for ørret i endel høyereliggende innsjøer i de sentrale østlandsområder. Det er lagt vekt på å belyse betydningen av regulering og konkurranse fra andre fiskearter, både pelagiske og littorale. For å vurdere avkastning, utsettingspålegg og produksjonsforhold vil det være av betydning å ha generell informasjon om tilgjengelighet av næringsdyr i ulike innsjøkategorier.

I en redigert utgave vil den foreliggende rapport bli publisert i et vitenskapelig tidsskrift. Redigeringen vil først og fremst omfatte figurene 2-5, da disse er å betrakte som en presentasjon av primærdata. Det er imidlertid i den foreliggende rapport valgt å presentere data fra enkeltsjøer separat.

Oslo, april 1988

Åge Brabrand

Svein Jakob Saltveit

INTRODUCTION

Habitat utilized by brown trout (Salmo trutta L.) in lakes is obviously influenced by the presence of potential competitors as well as by food selection and food items available. In most of the literature, brown trout are described as food generalists, but mostly take their food in the littoral zone. The availability of benthic food items is greatly influenced by the presence of littoral fish species and the degree of water level fluctuations. In lakes with several littoral species and large water level fluctuations, the availability of littoral food items may be scarce, and brown trout can behave more or less as a planktivore. However, the presence of pelagic fish species more specialized as planktivores may reduce the planktivorous tendency of trout.

In a regional study we have compared gut contents in brown trout from 15 lakes in the central part of South-Norway (Fig. 1). The lakes cover a gradient of water level fluctuations from unregulated to 8.3 m, and support four categories of fish communities (Table 1). In Category I, brown trout and minnow (Phoxinus phoxinus) are the only species present. In Category II, brown trout, minnow and whitefish (Coregonus lavaretus) are present, the latter as a planktivorous competitor (Svärdson 1976). In Category III, minnow and perch (Perca fluviatilis) are present in addition to brown trout, while Category IV have, brown trout, whitefish, minnow and perch. Perch behave both as a littoral competitor as well as a potential predator on minnow and juvenile stages of trout. In combination with the degree of water level fluctuations, the influence of littoral and pelagic food competitors on food uptake of trout is considered.

STUDY AREA

All lakes studied are situated in the alpine/subalpine areas in the central part of South-Norway (Fig. 1). Some hydrological and biological data concerning the lakes are given in Table 1. The outlet river of all the regulated lakes is unavailable for spawning, although recruitment is ensured through spawning in the inlet river or by stocking. Most of the lakes are classified as oligotrophic to ultra-oligotrophic, with total phosphorus concentrations below 30 µg/L. Temperature stratification occurs in the period June-September, with maximum epilimnetic summer temperatures in July.

MATERIAL AND METHODS

Trout for stomach analysis were collected overnight by sets of gill nets (1.5 x 25 m) in the littoral zone during summer (June, July) and autumn (August, September) from each lake. The following mesh sizes were used: 19.5, 22.5, 26, 29, 35, 39, 45, and 52 mm. When whitefish was present, pelagic gill nets (6 x 25 m) with mesh size 19.5, 22.5, 26, 29, 39, and 45 mm, and covering the depth interval 1-7 m below the water surface, were always used. However, in Røssjøen (cat.I) pelagic gill nets were also used.

Captured fish were measured, weighed, sexed, and their stomachs removed. Gut contents were analysed according to the volumetric method described by Hynes (1950). Fish from the littoral or pelagical zone were kept separate, and gut contents of up to 20 individuals from each 5 or 10 cm length groups were analysed.

Benthic communities were sampled from the stony littoral in all of the lakes during the period of fishing using the kick-method (Hynes 1961). Survey zooplankton sampling was carried out in all lakes with whitefish. Samples from the soft profundal and sublittoral bottom were taken using core samplers or Ekman grab.

Table 1. Investigated lakes, their altitudes (m a.s.l.), water level fluctuations (in metres), time of investigation and fish communities.

Lake		m a.s.l	Fluct.	Investigated	Fish community
Dokkvatn	1	776	N.R.[2]	July Sept.1978	Trout, minnow
Øyangen	2	676[1]	8.3	July Oct. 1977	Trout, minnow
Våsjøen	3	870[1]	3.0	June Sept.1986	Trout, minnow
Djupen	4	914[1]	3.0	Sept.1982 Sept.1983	Trout, minnow
Mjogsjøen	5	887	N.R.	July Sept.1979	Trout, minnow whitefish
Synnfjord	6	796	N.R.	Sept.1979	Trout, minnow whitefish
Goppollen	7	977[1]	2.2	Sept.1982 Sept.1983	Trout, minnow whitefish
Røssjøen	8	895	N.R.	July Sept.1978 July 1979	Trout, minnow perch.
Volbufjord	9	429[1]	3.0	July Oct. 1977	Trout, minnow perch
Dokkfløyv.	10	696	N.R.	July Sept.1978	Trout, minnow perch
Strandefj.	11	353[1]	7.0	July Oct. 1977	Trout, minnow perch,whitefish

[1]) Filled reservoir.
[2]) Not regulated lakes.

RESULTS

The main results clearly demonstrates the variability of food items observed in trout gut contents. This was highly related to food availability and inter- and intraspecific conditions both within each lake and between the investigated lakes.

Brown trout and minnow lakes (Category I).

Gut contents of trout in unregulated and regulated lakes where trout and minnows are living sympatrically is given in Fig. 2. In the only unregulated lake in this category, Dokkvatn, uptake of zooplankton by trout was insignificant, and was in summer completely dominated by nymphs of Ephemeroptera ("group other" in Fig. 2). In autumn, trout showed a piscivorous tendency, feeding to a large extend on minnows, which made up to 100 % of total gut volume in some length groups (Fig. 4). All other studied lakes in this category were regulated, and zooplankton was obviously an important food component at specific times of the productive period. However, during early summer, a diverse benthic animal community is also available in these lakes, while the zooplankton peak is somewhat later. Only in Lake Øyangen, brown trout fed on zooplankton as early as July, probably caused by the relatively higher water level fluctuation in this lake, giving low benthic animal densities, forcing trout to feed on zooplankton even in periods of low zooplankton abundance. In Lake Djupen, Daphnia longispina was of considerable importance in small trout, while the proportion of Bythotrephes longimanus increased in larger fish. Also in the regulated Våsjøen, the zooplankton component was dominated by D. longispina and B. longimanus. However, predation on the two species was more similar.

Brown trout, whitefish and minnow lakes (Category II).

Gut contents of trout coexisting with whitefish and minnow are given in Fig. 3. Three lakes are included in this group, two of which are unregulated. Zooplankton were not observed in the gut contents of trout from any of the lakes, either in July or in September/October. Trichopteran larvae were the dominating benthic group, together with a relatively high proportion of minnows, even in trout of size 15 - 20 cm. Fishing with pelagic gill nets showed a strong horizontal habitat segregation between pelagic areas completely dominated by whitefish, and the more littoral areas dominated by trout. This confirms the presence of a strong feeding segregation between trout and whitefish when coexisting.

Brown trout, minnow and perch lakes (Category III).

Gut contents of trout living together with minnows and perch are given in Fig. 4. In all the investigated lakes, the zooplankton species, Bythotrephes longimanus, was an important component of total gut volume, even in larger fish in some of the lakes. Compared to lakes with minnow, but without perch, trout predated on minnows to a much lesser extent, and when doing this, trout seems to be of larger size. In the unregulated lakes Røssjøen and Dokkfløyvatn, high availability of large benthic animals, such as Gammarus lacustris and trichopteran larvae is reflected in the high consumption of these food items.

Brown trout, perch, minnow and whitefish lakes (Category IV).

Gut contents of brown trout in the regulated lake, Strandefjorden, are shown in Fig. 5. Here brown trout coexist with the littoral living perch and minnow and the planktivorous whitefish. Regulation obviously forces trout to utilize both littoral and pelagic areas. However, water level fluctuations of 7 m will also have a very strong impact on the availability of benthic prey items. High densities of minnows and perch force trout to feed planktivorously in this lake, in spite of strong competitive pressure from a truely planktivorous population of whitefish. Both species fed to a large degree on _Daphnia_ and _Bosmina_, but trout also fed on benthic organisms such as Trichoptera and Chironomidae, as well as fish (largely minnows). Indeed, many lakes that posess perch, minnow and whitefish, have extremely low densities of trout, indicating a strong interspecific interaction.

DISCUSSION.

The availability of food items for fish is influenced by a number of factors, both abiotic (Aass 1973) and biotic (Klemetsen 1967, Langeland 1982, Nilsson 1960). General lake productivity, which influences status and species composition of both zooplankton, benthos and prey fish is of basic importance.

The most important feeding areas for brown trout in oligotrophic lakes are in the littoral zone. The high zoobenthic production here is due to vegetation, allochtonous inputs and temperature conditions. This zone is, however, vulnerable to drawdown of the water level, and important fish food organisms typical of this zone, such as _Gammarus_, snails and larger insects are affected (Grimås 1962). In general, impoundment can be divided into _short term_ and _long term_ effects. By increasing the water level, new areas rich in nutrients become available for production (impoundment effect). Few animals are however adapted to large seasonal fluctuations in water level. In the long term ice and wave erosion aided by freezing will lead to an inpoverished littoral zone, lacking vegetation and dead organic material for food and cover. There is therefore both a quantitative and a qualitative decrease in benthic animals in littoral areas (Grimås 1961, 1962). However, animals living in the profundal zone below the drawdown limit are not affected and may indeed profit by the organic material sedimented from the littoral zone. These benthic animals (chironomids, oligochaetes, mussels) are, however, less available to fish predation due to their habit of living down within the sediments.

More arctic conditions in reservoirs due to freezing in the littoral zone and deeper intrution of cold epilimnetic water during drawdown in winter, may lead to an increase in the importance of the crustacean Lepidurus arcticus in some lakes (Aass 1969, Borgstrøm 1973, Brabrand and Saltveit 1980).

Zooplankton production will increase due to increase in nutrients from the impounded areas and reduction in loss by closing the outlet. In the long term, this positive effect will disappear through grazing and sedimentation, but production of zooplankton will probably not be negatively affected (Elgmork 1970).

Despite the limits placed by the general productivity of lake ecosystems in determining the availability of food items, a number of authors have documented the influence of the fish populations themselves on prey abundance (Shapiro et al. 1975). Fish species have differing ability to suppress planktonic crustaceans and benthic organisms by their selectivity and changing predator pressure (Garnås et al. 1983).

In the subalpine lake, Øvre Heimdalsvatn, where trout were the only fish species until 1969, they feed on Bythotrephes longimanus and Daphnia longispina, and obviously selected food items from the zooplankton community at certain times of the year (Lien 1980). In the littoral zone, trout fed on Lepidurus arcticus and Gammarus lacustris, which are both sensitive to predator pressure (Brabrand et al.in prep.). The same planktivorous tendency is also shown by Klemetsen (1967) in Lake Jølstervatn. However, when whitefish are present, a switch in feeding habit in brown trout from partly planktivorous to a true benthic habit occurs, which only can be explained by interspecific segregation. This shift occurs both in regulated and unregulated lakes, because whitefish are more truely planktivorous than trout. Interesting, in most of the regulated lakes inhabited by whitefish, the trout population is small or even absent. An extreme environment is lake Trevatn, which is regulated approx. 7 m (Hellner & Saltveit 1981). In this lake, smelt are present in addition to whitefish, the former being even more planktivorous than whitefish, and probably forcing whitefish to feed more on benthic animals compared to the situation where whitefish are the only planktivorous species. The presence of smelt will therefore hamper further interspecific segregation between trout and whitefish, which in turn can leed to virtual absence of trout in this type of lake (Svärdson 1976). The only way for trout to survive in whitefish-smelt lakes is to switch to a higher trophic level, and changing to fish diet as often can be observed in a number of large lowland lakes in Scandinavia (Aass 1973).

However, as brown trout have the ability to utilize both pelagic and littoral habitats, it is the total environmental conditions which are of decisive importance for brown trout populations. In the present study, it is shown that trout can feed to a greater or lesser extent on planktivorous food, which is probably of special importance for immature trout. This will increase the intraspecific trout niche separation between immature and mature individuals. Also the effect of perch, a littoral predator, will be reduced, as they are primarily littoral predators (Popova & Sytina 1977). When regulated, the trout population of such lakes will adapt to an even more planktivorous behaviour, still maintaining high densities or even increasing, if spawning areas are not destroyed. This seem to occur independently of the presence of perch or minnow.

However, when perch and minnows are present, the potential of minnow as prey for larger brown trout is greatly reduced, compared to the situation when brown trout and minnow live alone. This aspect is probably of great importance, since minnow can obviously be an important food item for trout larger than approx. 15 cm, producing increased growth rates and intraspecific segregation for the trout population. Introduction of perch as a more effective minnow predator than trout, therefore seems to reduce the prey availability for trout themselves.

In conclusion, regulation has a serious negative impact on the brown trout populations when planktivorous fish species are present, notably regarding competition for food. The key elements here are a reduced benthic animal production and increased competition for pelagic food. Increased pelagic food competition together with wide water level fluctuations or presence of littoral fish species will reduce or even inhibit the trout population. However, trout may occupy a true pelagic predatory food niche, and can despite low abundance, reach large individual size.

Regulation of trout lakes lacking planktivorous fish species, give trout a pelagic feeding refuge, almost independent of water level fluctuations. Presence of littoral fish species or higher water level fluctuations increase the pelagic tendency of trout. In extreme cases, trout can turn into a completely planktivorous behaviour, also encompassing changes in morphology (Solheim 1987). A large population of trout in such lakes can still be maintained, or even increased after regulation. However, individual fish size are usually small, due to deficit of larger food items.

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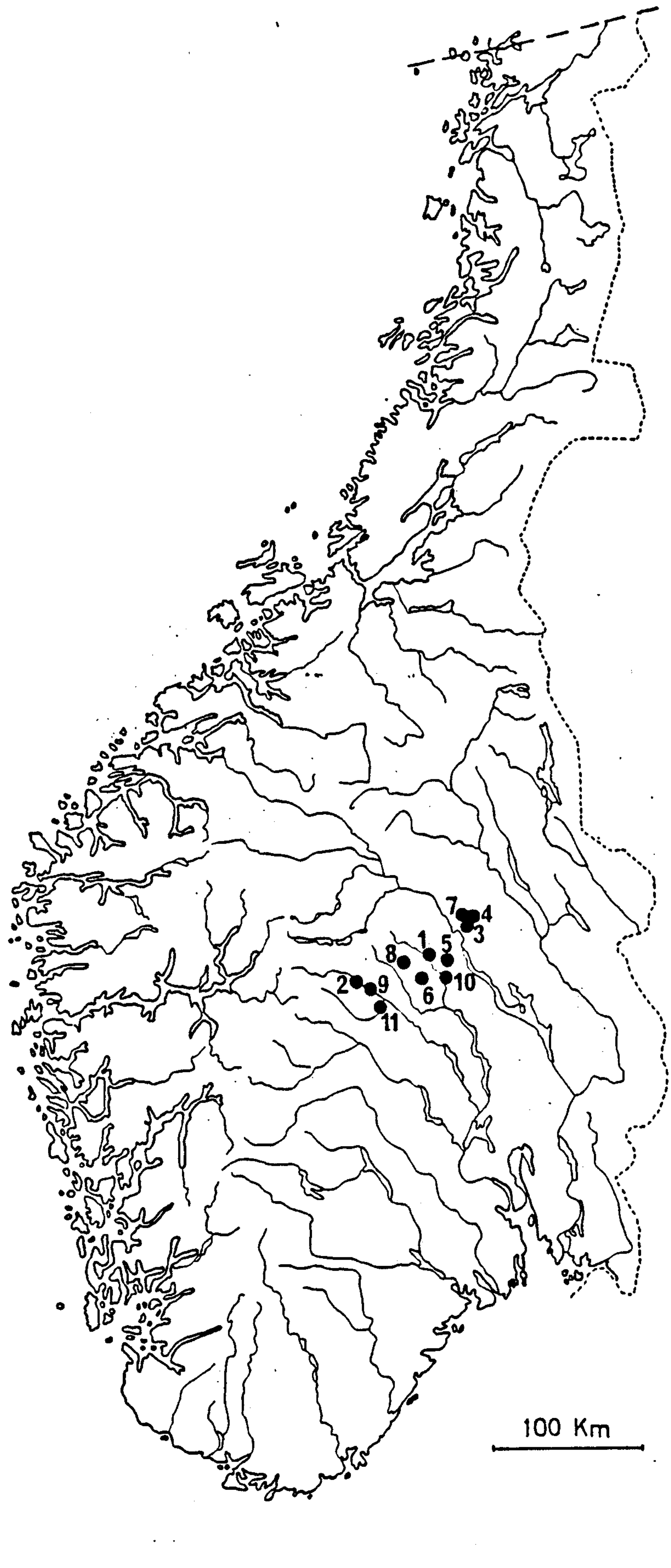


Fig. 1. Location of the investigated lakes, all situated in alpine/ subalpine areas in South-Norway. For identification of lake number, see Table 1.

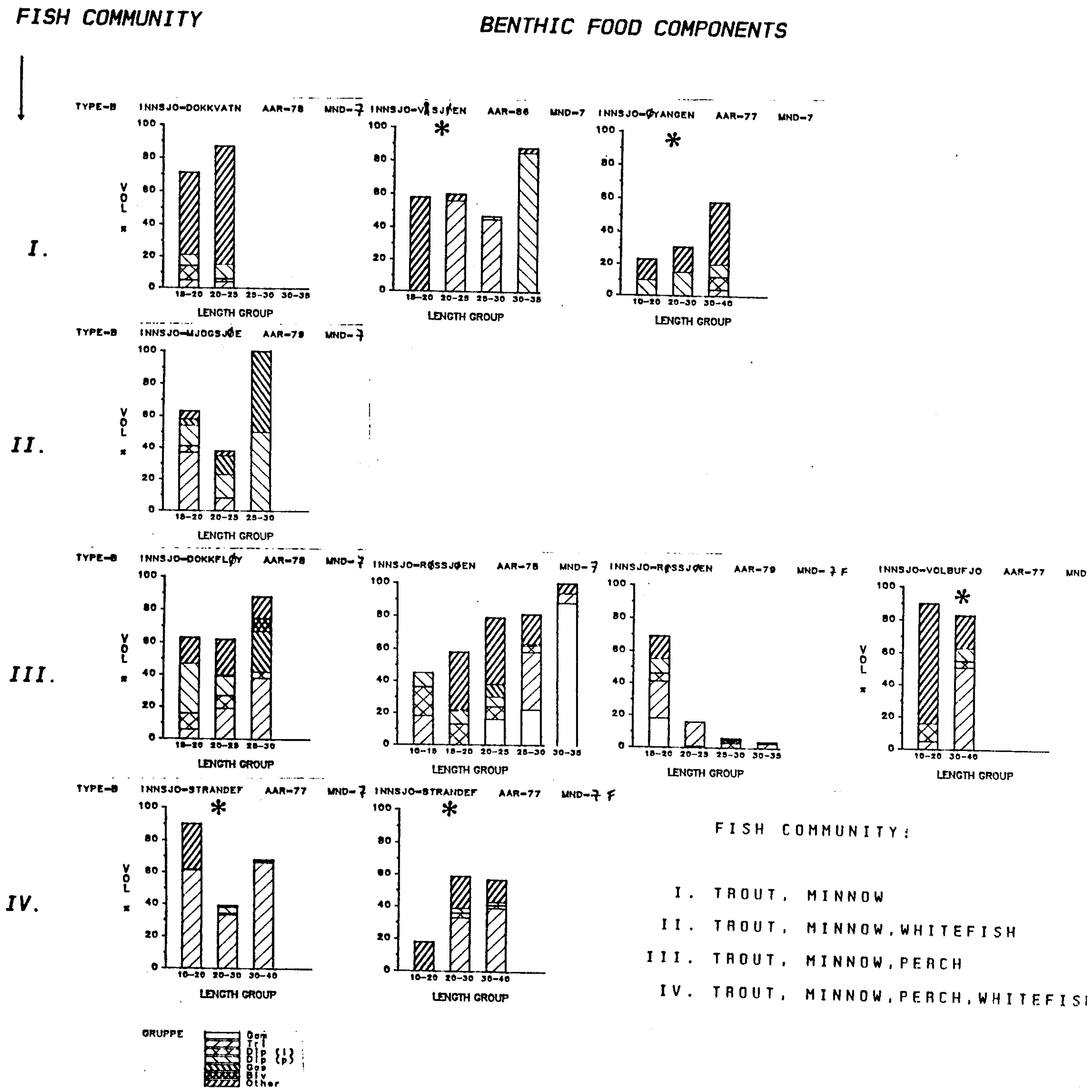
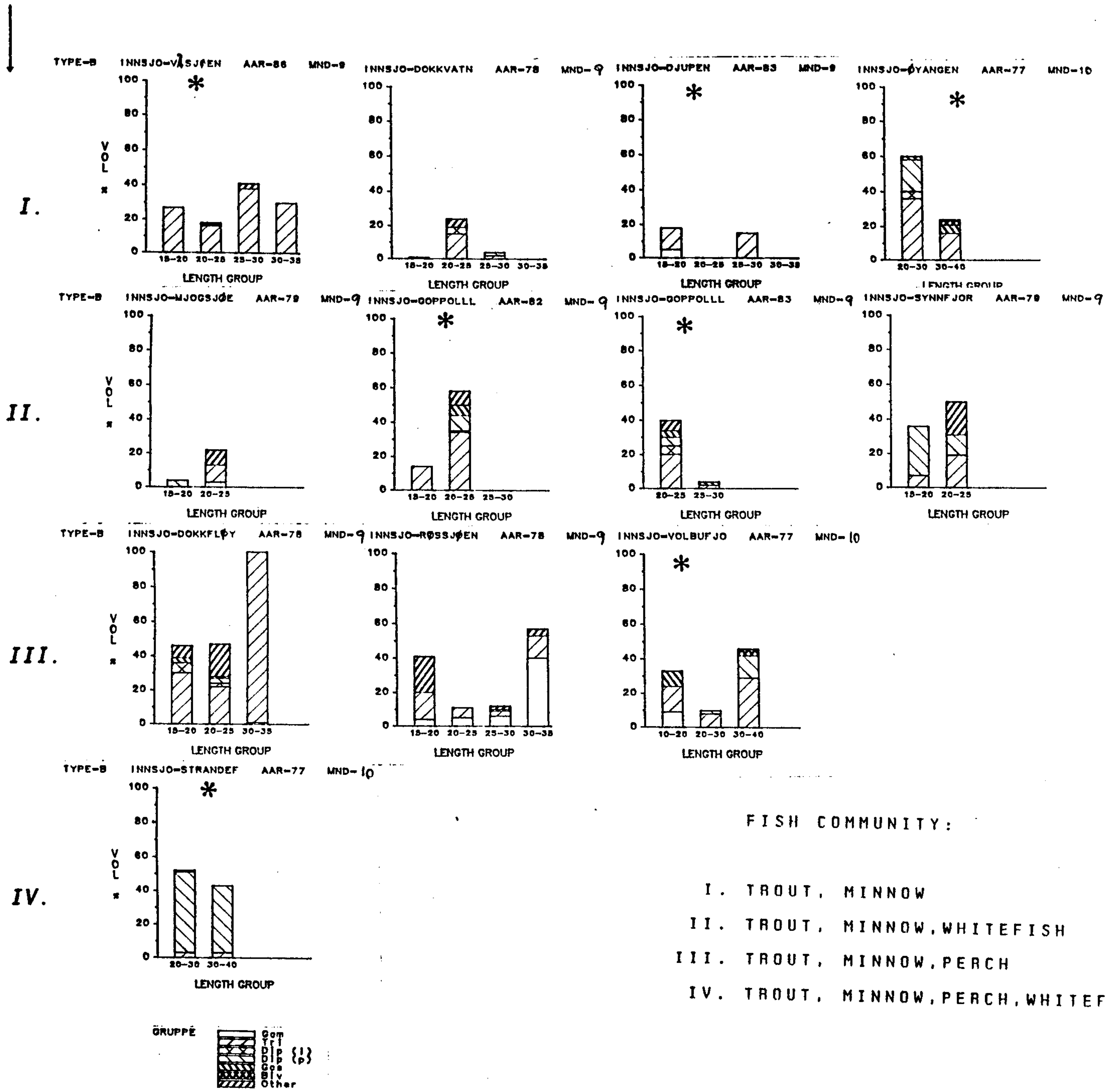


Fig. 2. Percentage of benthos of total gut contents of brown trout in early summer in lakes with different fish communities. Regulated lakes are indicated with an asterix.

FISH COMMUNITY

BENTHIC FOOD COMPONENTS



FISH COMMUNITY:

I. TROUT, MINNOW
II. TROUT, MINNOW, WHITEFISH
III. TROUT, MINNOW, PERCH
IV. TROUT, MINNOW, PERCH, WHITEFISH

Fig. 2. Percentage of benthos of total gut contents of brown trout during autumn in lakes with different fish communities. Regulated lakes are indicated with an asterix.

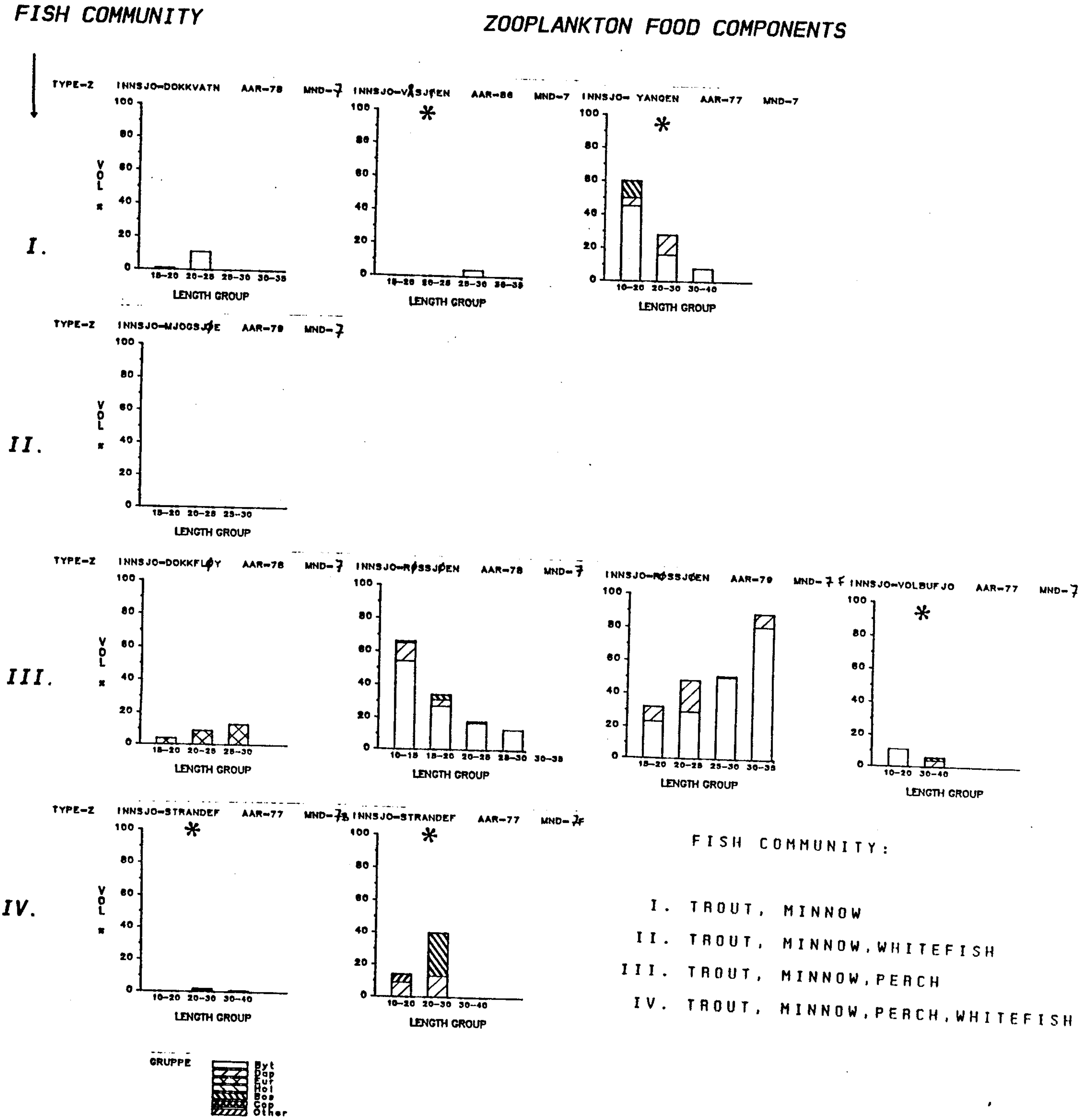


Fig. 3. Percentage of zooplankton of total gut contents of brown trout in early summer in lakes with different fish communities. Regulated lakes are indicated with an asterix.

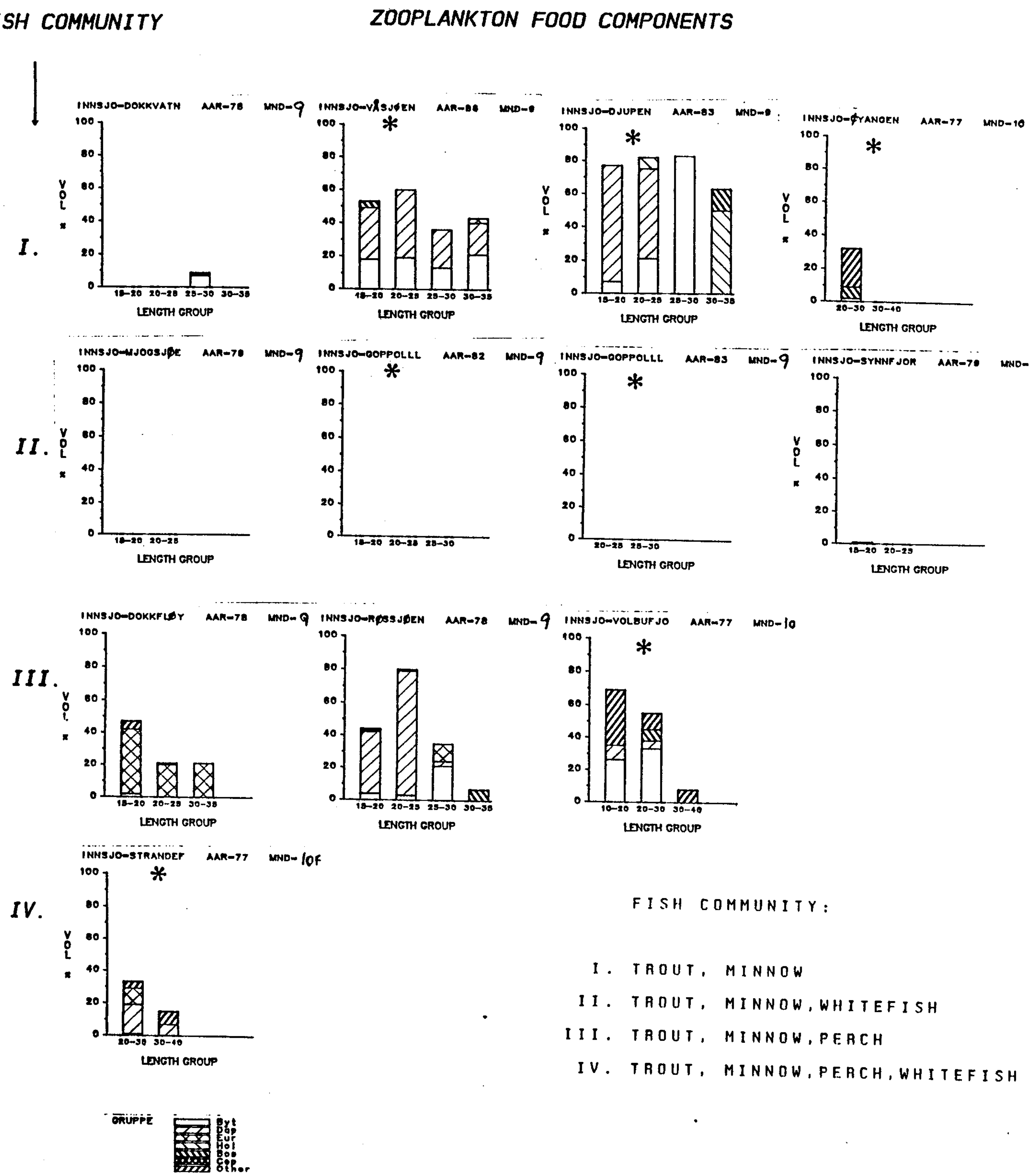


Fig. 3. Percentage of zooplankton of total gut contents of brown trout during autumn in lakes with different fish communities. Regulated lakes are indicated with an asterix.

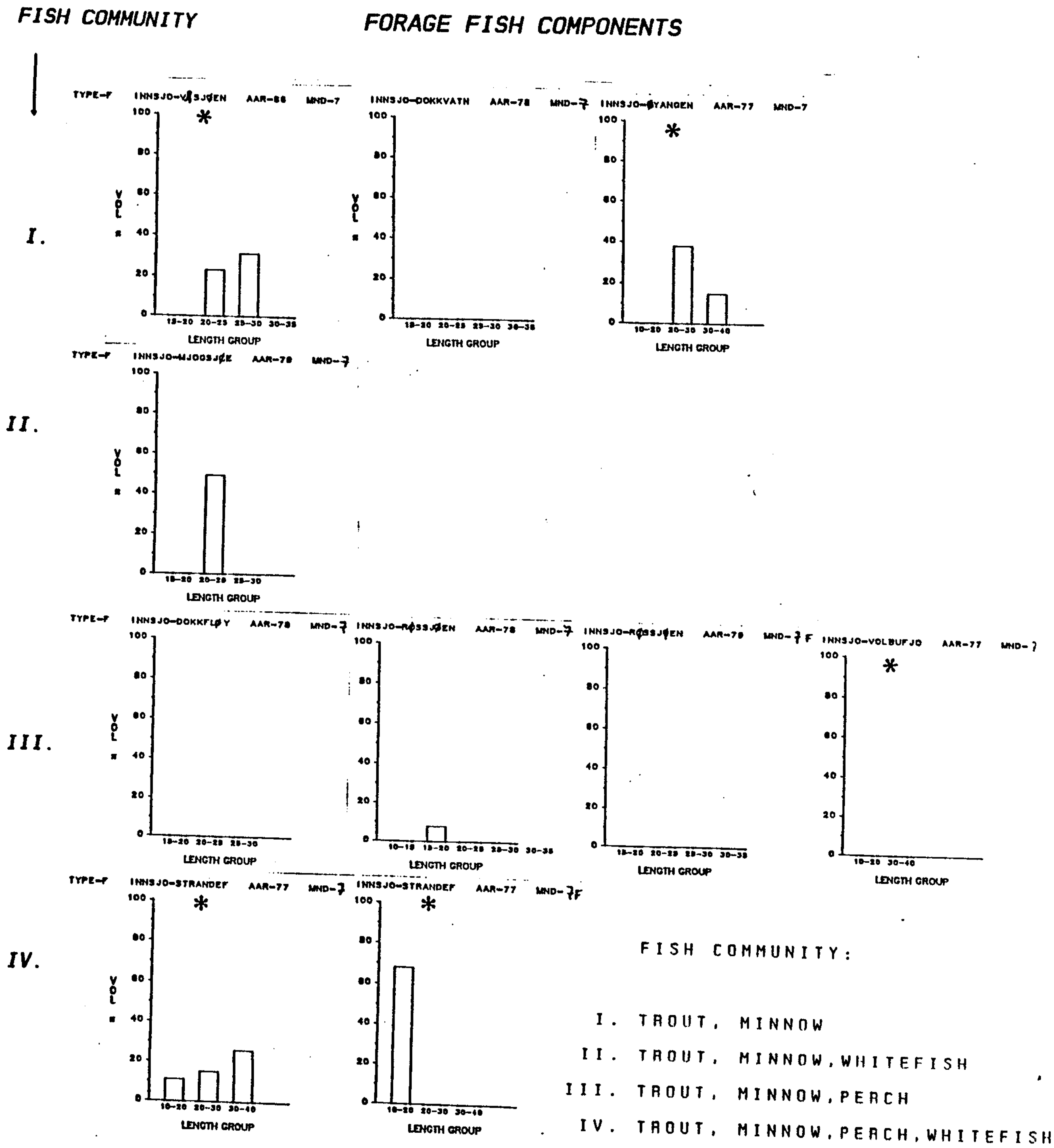


Fig. 4. Percentage of forage fish of total gut contents of brown trout in early summer in lakes with different fish communities. Regulated lakes are indicated with an asterix.

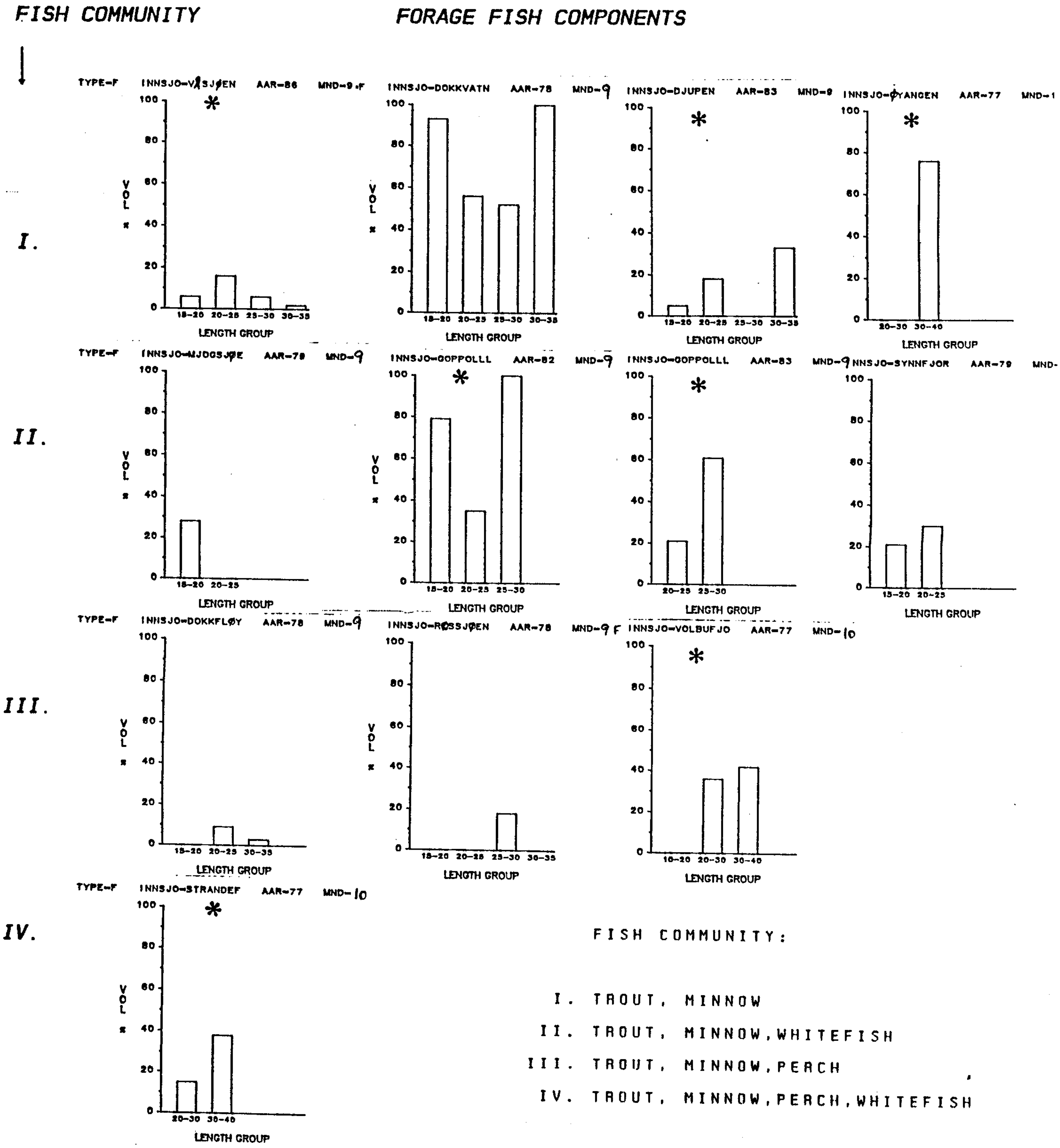


Fig. 4. Percentage of forage fish of total gut contents of brown trout during autumn in lakes with different fish communities. Regulated lakes are indicated with an asterix.

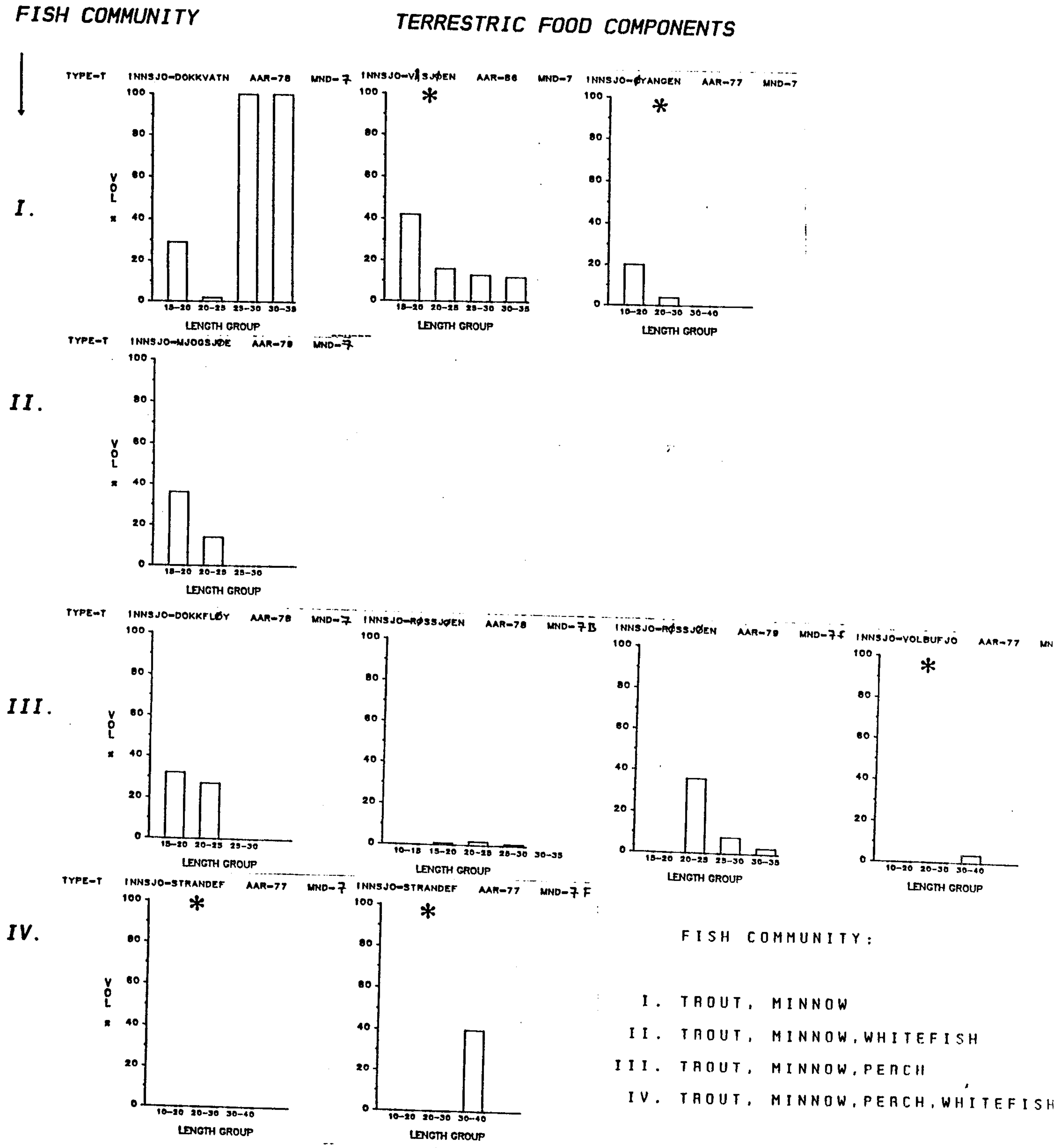
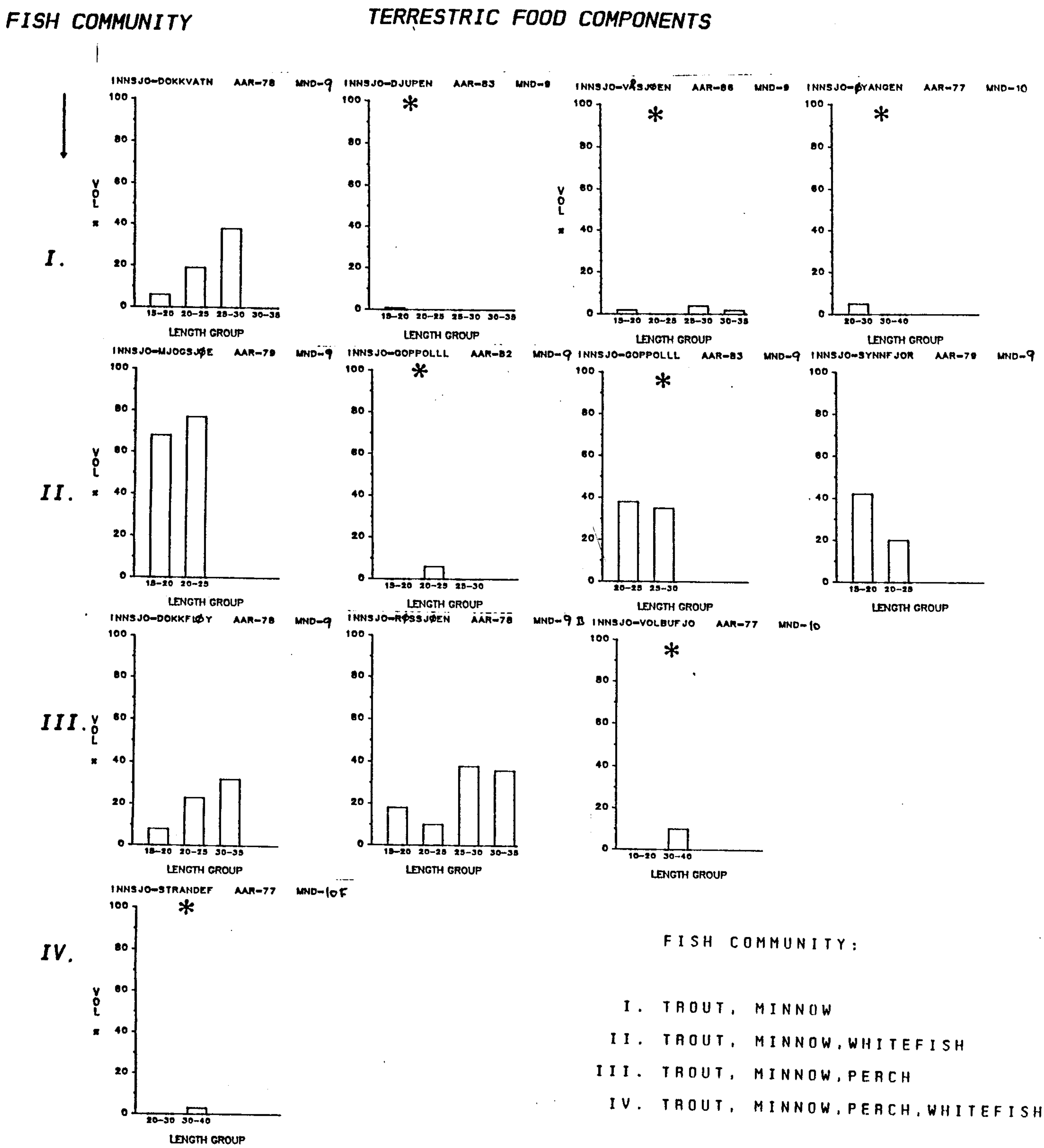


Fig. 5. Percentage of terrestric food components of total gut contents in brown trout in early summer in lakes with different fish communities. Regulated lakes are indicated with an asterix.



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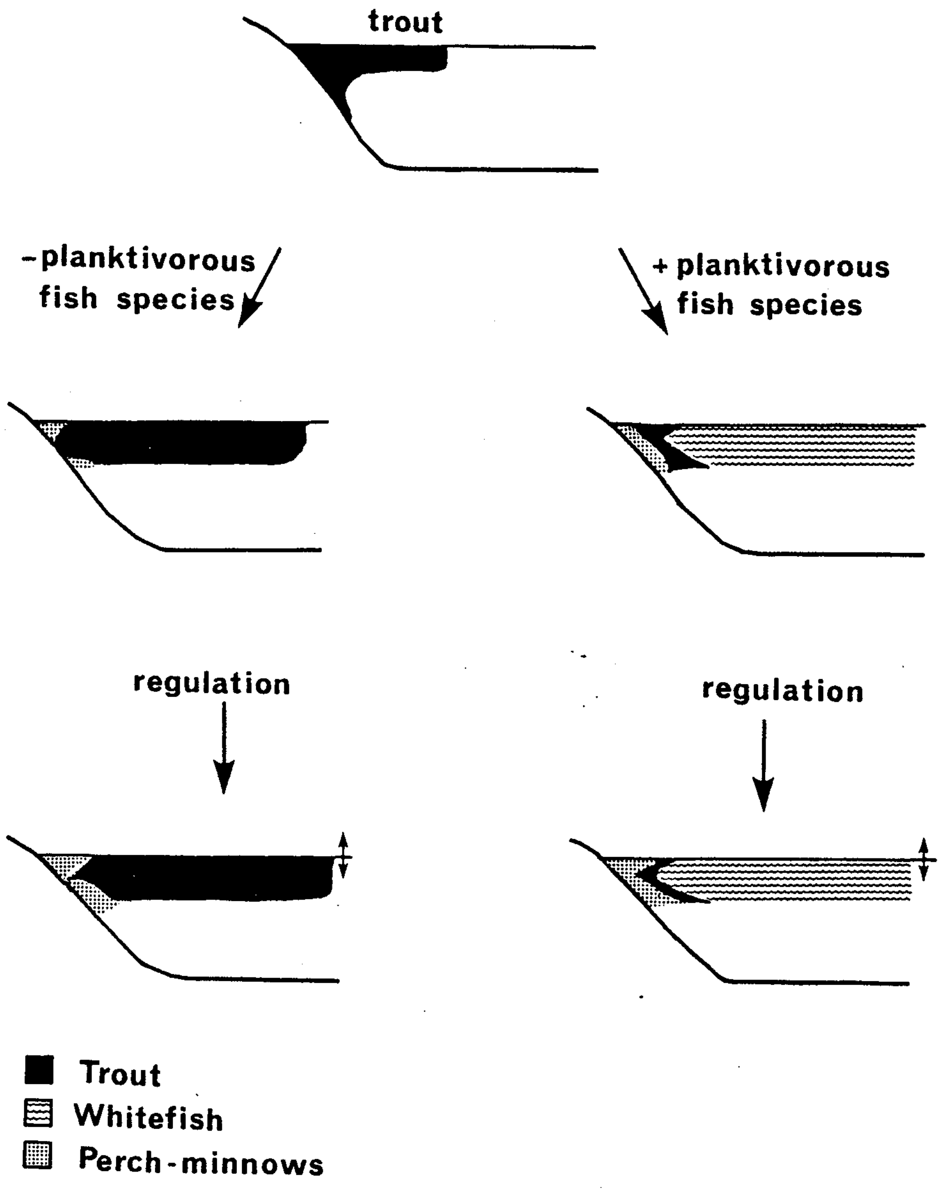

Fig. 6. Main pattern of habitat available for brown trout (Salmo trutta) in absence and presence of littoral and pelagic competitors. Regulation is indicated by an ↑ .