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Selective plankton feeding by the coregonid "bondella" (*Coregonus* sp.)
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Introduction

The problem of feeding selection is interesting and of great importance from the viewpoint of a more correct interpretation of the phenomenon itself and of that of its energetic implications. In the particular case of fish, instances of selection have always arisen in the numerous researches aimed at their feeding habits. Nonetheless, only in relatively recent times, have some specialists begun to study the subject of food selection in an organized way, thus highlighting its importance. Among these it seems appropriate to cite in particular: Brooks, 1968, 1969; Brooks & Dodson 1965; Dodson 1970; Hrbáček 1962, Hrbáček et al 1961; Galbraith 1967; Jacobs 1961, 1965, 1966; Zaret 1972 a and b. These researches have demonstrated how the pressure of selective predation by fish on zooplankton populations, influences both seasonal abundance and population structure.

In the present work, I intend to evaluate the impact of predation on the eupelagic zooplanktonic biocenosis of Lago Maggiore, producing, in this way, as far as possible, a basis for a better understanding of the population dynamics of the species of zooplankton directly involved.

Another aspect which has been studied is that related to the mechanism of selective capture set in action by the predator. To this end we have sought to bear in mind that the subject should be interpreted as a function of numerous factors acting contemporaneously, that is as the interaction of characters peculiar to the predator and to the prey (Ivlev, 1961).

Material and Methods

The species studied, locally called "bondella", belongs to the family Salmonidae, subfamily Coregoninae and was introduced into Lago Maggiore in 1950. In a short time, this coregonid acclimatised perfectly, establishing a clear advantage over a pre-existing form of coregonid commonly called "lavarello" and which was introduced at the end of the last century. In the course of a few years, the "bondella" established itself as the dominant pelagic species, reaching up to 180 tons of fish per year.

The fish in this study have always been caught in the neighbourhood of Cannero, fortnightly from April - the month in which the coregonids start feeding again with regularity after the winter - to December 1972, with nets of mesh aperture 35 mm, that commonly used by commercial fisheries for the coregonids. The use of this mesh guarantees the capture of adults, of constant dimensions - and hence of age - (length: 25-30 cm, age 2-3 years) - in order to avoid interference from possible differences of food selection according to size.

After making the customary morphometric measurements, the body cavity was opened for excision of the stomach and oesophagus. Each

stomach was then emptied of its contents and weighed in its entirety, after which a subsample was withdrawn weighing about 50 mg from which the various organisms present were evaluated.

From microscopic examination of the gut contents, one can never detect irregularity in distribution in the gut of the organisms of the different zooplankton species; this fact gives some validity to the calculations made from subsamples. Of a total of 500 stomachs examined, 200 were rejected because the contents were digested to such an extent that they were of little value.

For some fish, the co-efficient of ripeness ($Cr^0/00$) was calculated and also the number of planktonic individuals per kilogram of fish (NiKgp) (Pavlovskii, 1961): by these expressions, one derives the mean percentage composition of the different species eaten. The results are given in Fig. 1.

From the gut contents, preserved in 4% formalin, 50 individuals were taken out and measured on the screen of a microprojector. Length of cladocerans was taken from the anterior edge of the head to the point of insertion of the tail-spine and of copepods from the anterior edge to the furca. It was not possible to measure Leptodora accurately because its delicate structure is deformed or incomplete. The results are given as means with confidence limits.

At the same time as the fish were caught and at the same place, zooplankton samples were taken in order to have a picture of the food available to the fish. This sampling was done by means of a sinusoidal

haul between 0 and 50 metres depth with a Clarke-Bumpus sampler fitted with a net of mesh aperture 350 μ m. The material captured was diluted [Ital = diluito] to 100 ml, from 20-30 of which, counts were made on cladocerans and copepods. Fig. 2 shows the percentages of the various organisms eaten. As was done with the gut contents, 50 specimens of each species were measured. The results were then synthesized with the same statistical parameters.

Examination of the collected material.

Food selection and seasonal periodicity.

Fig. 1 shows the variations in mean percentage composition of the gastric contents during the sampling period. In April, the food consists almost entirely of organisms of the genus Cyclops⁽¹⁾: by May, one detects a shift in feeding towards Daphnia hyalina, while the genus Cyclops takes second place. In June, Daphnia hyalina is the one animal most often found in the stomachs, and the same situation is true of July. In this period, nevertheless, the predatory cladoceran Bythotrephes longimanus begins to appear and is important as food from mid-July to the end of October. During August, September and October, the other large predatory cladoceran of Lake Maggiore, Leptodora kindtii also appears in the fish stomachs; however Leptodora in these three months has never exceeded 10%, and during the same period the percentage of Daphnia ranged from 10 to 15%. In November, high percentages of Daphnia are again found and in December Cyclops is strongly preyed on.

The presence in the stomachs in December of Eurycercus lamellatus,

(1) The two species Cyclops strenuus and Mesocyclops leuckarti were not separated because it was difficult to see the distinguishing characters in the digested material from the fish stomachs.

a typical littoral form is probably understandable if it is borne in mind that approaching the season of reproduction, the coregonids tend to migrate from deep into shallow water.

Thus, from May to November, the food of the fish is found to be almost exclusively derived from the cladoceran population, with a distinct predominance of Daphnia hyalina at first during the coregonid growing season (May, June & July) and of Bythotrephes in the succeeding three months.

In April and December, cyclopoid copepods are included in the diet.

Comparing these results with those of Berg and Grimaldi in 1962-63, a substantial agreement is noted regarding the succession of different species and their importance in the growing season and in the diet of the fish.

We consider next the availability of food offered by the zooplankton in the zone of the fish (fig. 2). As already noted, the food consists mainly of copepods and cladocerans, rotifers never appearing in the stomachs.

The most important part of the plankton, from the point of view of numbers, are, in Lake Maggiore, the copepods (Tonolli 1962; Bonacina, personal communication). This result is verified also in the histograms in Fig. 2: indeed, in this, one can see that the percentage of the population of Cyclops and Diaptomus, relative to the total population examined, lies between a maximum of 98% in April and a minimum of 51% in September. Nonetheless, the coregonid, in the period of the year

when it puts on most weight, feeds exclusively on cladocerans. The only months when predation is mostly on copepods, are April and December. Also in this instance, the fish feeds selectively on Cyclops, even though these are less numerous than the diaptomids.

Regarding cladocerans, percentage values of Daphnia hyalina are highest from May to early July and the predation by fish at this time is highly selective for Daphnia, especially in June.

The observations on Bythotrephes are of great interest. Although this predatory cladoceran forms at most 0.84% of the available planktonic food in the lake, it forms up to 80% of the gut contents.

Similar evidence can be established for the other predatory cladoceran, Leptodora kindtii, with percentage values in the lake not exceeding 0.69% but in the guts from 4 to 10%.

These observations seem to show that the fish actively search for their preferred prey as they relate to two pelagic cladocerans which, as is known, do not form swarms.

The cladoceran, Diaphanosoma brachyurum, which in July, August and September has considerable population densities is completely overlooked by the fish.

For the purpose of quantifying the selective activity of the fish from comparison of the food in the guts to that in the water, we have used the electivity index of Ivlev (1961). This index, as is known, has values from +1 to -1, expressing, in this way, the whole range of

electivity which ranges from particularly intense search for one particular organism to total rejection. The three organisms for which the electivity index is always positive are Daphnia hyalina, Bythotrephes longimanus and Leptodora kindtii (Fig. 3). For the cyclopoid copepods, except for the two positive results in April and December, values are negative and very often equal to -1.

When these electivity indices are studied in more detail, it appears that the fish exert a distinct selection for Daphnia early in summer when Leptodora & Bythotrephes are not present in the water-mass. When Leptodora & Bythotrephes are present, the fish show a clear preference thereby relieving the predation pressure on Daphnia which takes a subordinate role in the fish diet without however being ignored as a food organism of first importance.

Intraspecific size selection

We proceed now to see if, in the living-space of each planktonic prey species, one can detect a preference by the fish, for organisms of larger size.

Fig. 4 shows graphically the mean lengths, with relative fiducial limits, of individuals of Daphnia hyalina found in the gut contents and of those from waters of the lake. The mean length of those eaten, taking into account the whole sampling season, are larger than those present in the natural population. This phenomenon tends to be accentuated towards the second half of July when the fish predation is especially heavy on organisms of the large size of Daphnia.

Fig. 5 shows the same parameters for the species Bythotrephes longimanus. Size selection is not so obvious as it was for Daphnia: comparison of relative mean values for the period up to early August shows on the contrary that Bythotrephes in the lake were larger than these in the fish stomachs whereas in the following months this relationship was reversed.

Absence of size selection of Bythotrephes in the period when it is numerous can perhaps be attributed to the fact that this organism has an indispersed distribution and is never very numerous especially in early summer. Consequently, size selection would seem incompatible with the active search of a really hungry predator. The situation is reversed in autumn with increase in population density of Bythotrephes.

Comparison of Figs 4 & 5 shows that the mean length of the Daphnia eaten undergoes a sudden increase at the time when the Bythotrephes appears as an alternative food: the Daphnia found in the stomachs are much larger compared to the mean length of the lake population and very much nearer to that of the Bythotrephes eaten by the fish.

For the reasons already given, no Leptodora were measured.

From the literature (Berg & Grimaldi, 1965, 1966; Grimaldi 1969, 1972) and in part, from what has been shown here, the food of the coregonid during winter and spring, in spite of being small in amount, is found to consist of Cyclopidae. Because of the inadequate material from the stomach contents, distinction between the two species

Cyclops strenuus & Mesocyclops leuckarti was made difficult and also between the adult and the copepod instars. Nonetheless there is little of significance to compare the size of these predators and those of the natural population. On the other hand, the lengths of the individuals caught in the lake and identifiable as Cyclops strenuus (Fig. 6) can be compared with those of the other food organisms. One can thus see that the mean dimensions of these populations are constantly inferior to those of Daphnia & Bythotrephes.

The size measurements of the diaptomid copepods and of the cladoceran Diaphanosoma brachyurum - zooplankters which, as has already been stressed, are not subject to much predation by the coregonid - show how much their mean lengths are inferior to those of all the organisms on which the fish actively preys. (fig. 6).

To sum up, the data given above are to be summarized as follows:

- in the period under consideration, there is a successive concentration of predation on those organisms which, contemporaneously, achieve in the lake larger size.
- size selection of a species seems to assume particular importance only for Daphnia hyalina. This consideration acquires greater prominence when one bears in mind that the mesh of the net used for collection of zooplankton caught mostly the adult portion of the population of this cladoceran. It follows that coregonid predation is limited, not simply to adults but to those among the adults which are largest in size.

DISCUSSION

Hypotheses on the dynamics of capture and selection.

It is an interesting problem and, as yet, not clearly resolved. The first hypothesis which at once can be made is that the branchiospinal apparatus of the planktophagous fish is the selective instrument of the kinds of zooplankton. Some researchers have tried to estimate the selective efficiency of this apparatus (Yoneda & Yoshida 1955; Hiyama and Yasuda 1957; Galbraith 1967; Kliewer 1970) without however being able to establish a clear relationship between the spaces of filtering structure and the dimensions of the prey. In this regard, one should note that often in these works the width of the branchiospinal spaces have been compared with the length of the ingested organisms, no account having been taken of the possibility that these may have been orientated in front of the filtering apparatus according to their minor dimensions: width and depth.

A more general objection can be raised to such theories: the branchial spines are covered with a film of mucus which notably reduces the spaces between these spines. One should observe also that the zooplankton are in general furnished with setae, more or less numerous and often of considerable length, which would contribute to trapping of such an organism in the mucus regardless of its actual dimensions. It seems therefore very difficult to maintain that the branchiospinal apparatus can carry out size selection in the range of a few tenths of a millimetre. Moreover, as described already in this research, the coregonids, in the springtime feed almost exclusively on cyclopoid copepods; these are much smaller than the daphnids which, in the following months should be ignored as food organisms. If, therefore, the branchiospinal

filter could exert dietary selection from prey-size, it would be even more difficult to explain, from a purely mechanical viewpoint, a similar variation in the external dimensions of the captured organisms.

Many authors have advanced the hypothesis of visual selection. It is important therefore to make clear that the selection takes place always between organisms which are almost without colour and often transparent.

Several authors (Brooks 1965, Hrbáček 1962, Green 1967, Jacobs 1961, 1965, 1966; Zaret, 1972 a and b) support this hypothesis, mainly on the grounds of the morphological modifications observed in zooplankton populations as a consequence of predation. Brooks affirms that the phenomenon of cyclomorphosis, which can be seen in Daphnia populations in some lakes, is largely determined by the selective predation to which they are subjected. Indeed this author holds that the development of the helmet has the effect of maintaining at a moderate size that part of the body, especially the brood-chamber, which, because of the strong colour contrast with the transparent body, constitutes a region of greater conspicuity.

Zaret, on the basis of field data (1972a) and laboratory results (1972b), proposes that the differential predation exerted by a cichlid on two diverse forms of Ceriodaphnia cornuta may be associated with the greater visibility of one of them, and it is indeed the form in which the dark ocular zone covers the greater area which is more intensely preyed upon. Jacobs (1965), observing a diverse frequency of antennal beat in two forms of Daphnia galeata mendotae, surmised that the consequent different character of swimming activity would render the more active

form more visible and hence more subject to predation.

These hypotheses revive a particular interest, in as much as they find theoretical support in the assumption that planktophagous fish feed exclusively by sight (Brooks 1968: Ivlev 1961: Lindström 1955; Nikolsky 1963). In the experimental work of Ivlev, for example, it appears that non-living food is ignored and that the predator is aroused to strike by the movement of the prey. Movement and size are also indicated by Lindström (1955) as the only characters which can influence the feeding preferences of the predator. These experimental observations are confirmed by physiological studies on the eyes of these fish (Brett 1957) whose results indicate that this organ is specially adapted to the perception of movement and is indeed deficient in distinguishing shape.

Considering these premises, it is perhaps permissible to allow that an organism or a species of zooplankton which is characterised by movement different from that of other species present contemporaneously in the same water-zone, through greater speed and change of trajectory, can stimulate the response of planktophagous fish to such an extent as to become, electively, the object for predation.

In effect, from the observations presented in the present research, it turns out that the organisms subject to predation are selected from those which are larger in body-size and have more conspicuous swimming movements, for all that they may not be the most abundant organisms among those present in the area in which the coregonids are feeding. The zooplankters with these requisites would have then the disposition to arouse the capture-stimulus of the fish because their displacements

would have acquired a greater prominence against a background made up of organisms more numerous and characterised by similarity of movement. Let us examine now, for the results collected over the whole sampling period, how selection varies with seasonal succession. In general, food selection by the fish seems to be a direct function of the dimensions of the available prey and of their motility, functions inverse to their density. Moreover, Cyclops, Daphnia, Bythotrephes and Leptodora which alternate during the year as principal objects of food, constitute, in the period under consideration, a succession with characters increasing throughout as regards size and speed, and decreasing for density. These observations lend support to the hypothesis that these factors play a determining role in the direction of predation and would also help to explain the sudden transition in the food regime from one species to another in the series preceeding.

As regards the size selection observed on the population of Daphnia hyalina, one should note that the adults of this species, individuals that is of size in the region of 1200-1300 μ , have swimming speeds greater than their young. (Dr. Bernardi, personal communication) which, for the same reasons as stated, comes to form part of that hypothetical background of organisms with limited powers of swimming which would be better explained by assuming that the adults move in rapid jerks.

Particular interest lies in the fact that when a species appears which greatly stimulates the predatory instinct of the fish, the species preceding it as food comes to be practically ignored as a

food organism (for example, passage of the feeding from Cyclops to Daphnia). This evidence seems to suggest a kind of adaptation and adjustment of the visual receptivity of the fish to a higher level of awareness. Indeed, when the predator turns to feed on Bythotrephes, the mean length of the Daphnia which continue to be preyed on, although with less intensity, increases notably, as if only the movements of these larger Daphnia could succeed in arousing the predatory instincts of the fish, by this time adapted to the movements and to the dimensions of the Bythotrephes.

Effect of the selective predation on the zooplankton population of Lake Maggiore.

First of all to start the discussion on the possible effects and on the significance of the selective predation of the coregonids on the zooplankton population, we take a quick look at the trophic level occupied by the species involved in the food chain in question, and at some simple mechanisms which regulate their population dynamics. For this purpose, we adopt the scheme proposed by Brooks (1969) in which, for simplicity, the filtrators of the zooplankton (Diaphanosoma, Daphnia, Bosmina, Diaptomus, and Rotifera) are regarded as herbivores; the cyclopoid copepods whose feeding habits are little known, are classified at an intermediate level between filtrators and predators since many may seem to choose small animals rather than filter particles; Bythotrephes and Leptodora, finally, are classed as predators on zooplankton of small size (Fig. 7).

The populations in question are found in a dynamic situation,

in the final analysis regulated by birth and mortality.

Natality, apart from factors characteristic of each species, is regulated by variable physical and chemical factors and especially by the kind and amount of available food. The food supply does not favour in equal measure all the species present in the water of the same trophic level, but in particular those which succeed in gaining an advantage in the competition for food. Cladoceran filtrators of large size (Daphnia) for example appear to be more successful than those of smaller size (Bosmina, Diaphanosoma) either because the filtering apparatus can select particles of larger size or because of more efficient use of the food (Brooks & Dodson 1965; Burns & Rigler 1967).

As regards mortality, we must distinguish between natural mortality and predation. The first is maintained, generally, at a somewhat low level and its variability is linked, more than the other, to seasonal progression. If, then, only natural mortality were to act on the population, this would tend to stabilise, each time around about the highest values of development permitted by the available food at that time.

Mortality from predation on the other hand is made plain by a sharp fall in population accompanied by high food availability and a high birth rate. It is evident then that predation has the function of restraint on a population with considerable capacity of expansion. If predation, as in the case of planktophagous fish, is turned to zooplankton species of large size, it will in consequence balance, or, if very strong, wipe out the advantage which large species may have over small ones when competing for the available food.

Profound changes in composition of the species of zooplankton have followed the introduction of fish into small lakes (Brooks 1968; Brooks & Dodson 1966; Cramer & Marzolf 1970; Galbraith 1967; Hrbáček, Dvorakova, Korinek, Prochazkova, 1961; Hutchinson 1971). These authors have been able to demonstrate clearly that in the lakes of small size examined by them, when there is no selective predation, large species of zooplankton predominate and those of small size are competitively eliminated in search for food. If there is only modest selective predation on the larger species, expansion of the larger species is moderated, and development of smaller species is encouraged. Finally, when predation is particularly intense, the smallest species can develop, species which avoid predation, and become dominant.

We will consider now the situation in Lake Maggiore throughout the period of this research. Bearing in mind that the limnological characteristics of this lake are very different from those of small lakes considered in the cited works and moreover that the population dynamics of the zooplankton are much more complex, one can state that the strong size selection of which Daphnia hyalina is the object is not sufficient to limit irreversibly the developmental capacity of the population of this species, but it is yet enough to offer to small cladocerans, Bosmina coregoni and Diaphanosoma brachyurum, kept back in direct competition with Daphnia, a possibility, albeit modest, of development. A factor which complicates considerably the interpretation of the effect of the predation by the coregonids is the presence in the pelagic trophic network of two predatory cladocerans, Bythotrephes and Leptodora. These species, which experience strong predation during their first seasonal appearance

from the coregonids recover to maintain for some months a notably stable population which prey on small cladocerans and young stages of Daphnia (Mordukhai-Boltovskaya 1958). Daphnia populations are subject then to two types of predation of different significance. The first is that made by coregonids on the adults and hence on reproducing individuals; the second by Leptodora and Bythotrephes is directed towards the young stages that is those which will give rise to adults.

It is concluded that in order to be able to give a precise estimate of the effect of coregonid predation, it is essential to carry out research on the dynamics of the populations which take part in this non-linear food chain. It is interesting to observe how the diversity and complexity of the system increase with onset of the warm season, as a real incentive to the highly selective size predation formed by planktophagous fish. Indeed, according to some authors (Dodson 1970; Paine 1966) predation by fish on the larger herbivorous organisms (in this case adult Daphnia), determines, by diminishing competition for food, a larger succession of the smaller herbivorous organisms, including the juvenile instars of Daphnia. The advantage in feeding thus gained by the cladocerans, Bythotrephes and Leptodora, by the greater density of those small plankters on which they preyselectively, would be offset by the effects of fish predation to which, Bythotrephes and Leptodora are, in their turn, subjected.

In the end, the coregonid, on account of a situation instigated

by itself, would be able to use, through the pathway of the large predatory cladocerans, the contained energy, otherwise not available, of the small herbivorous zooplankters.

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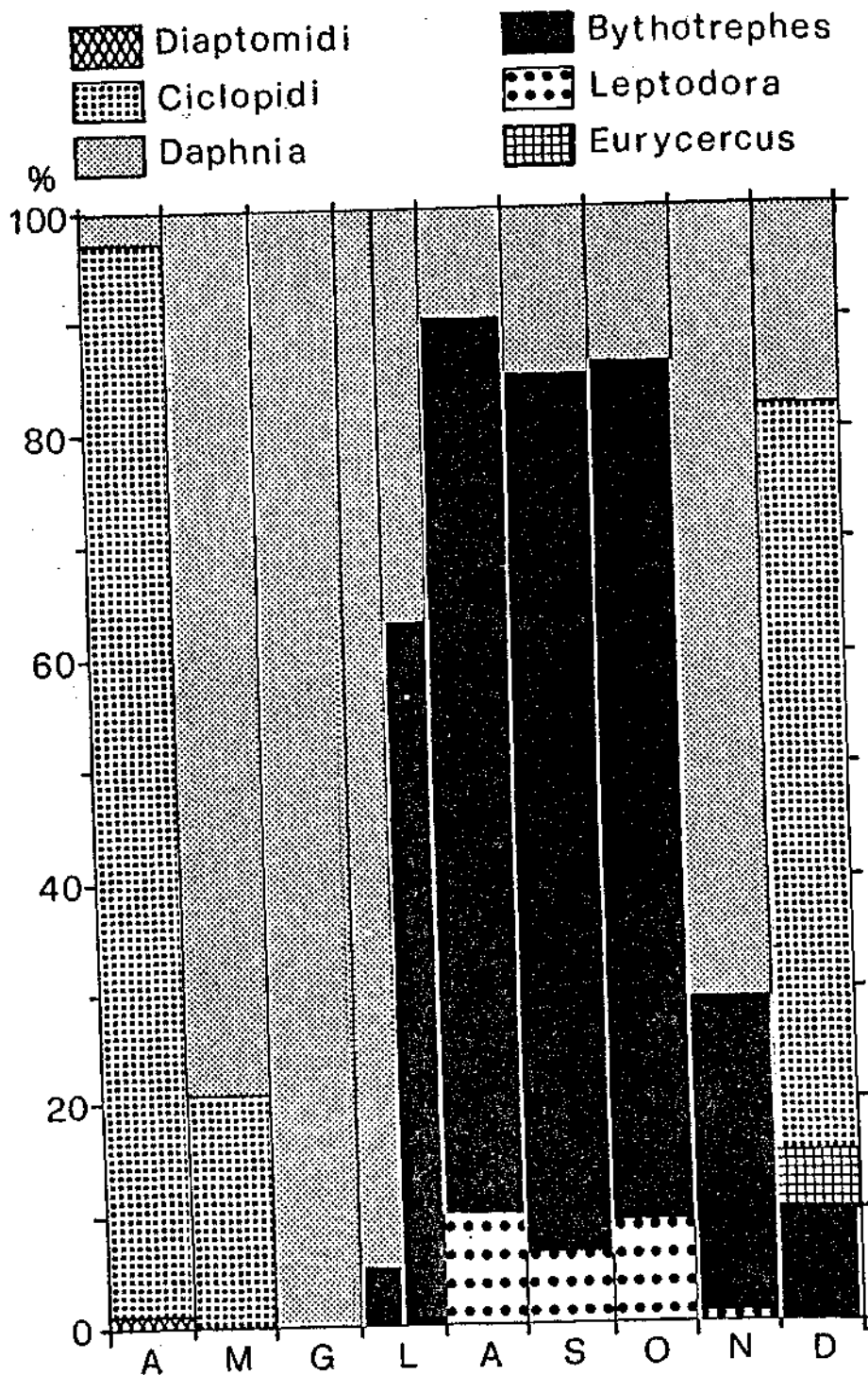


Fig. 1. - Contributo numerico degli organismi zooplanctonici nel contenuto gastrico

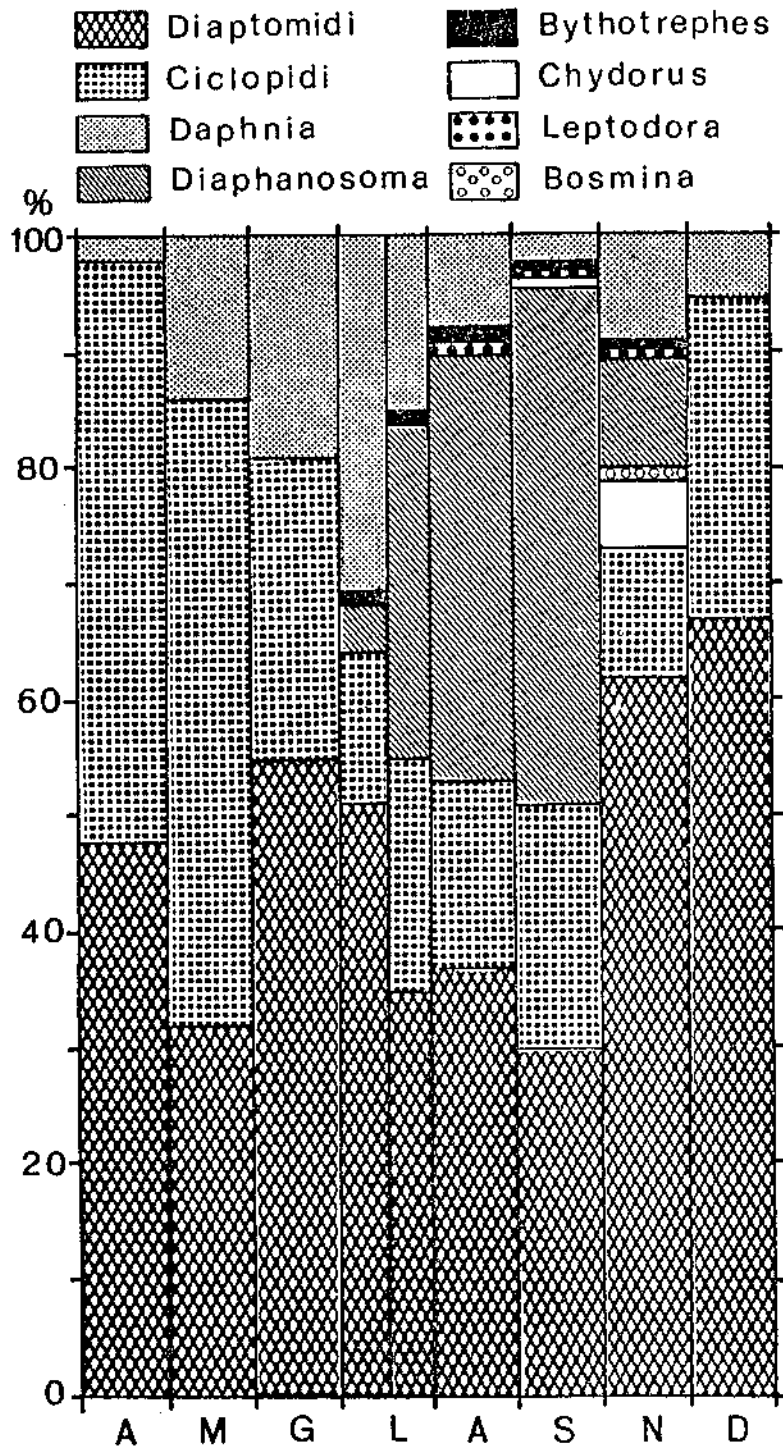


Fig. 2. - Composizione percentuale del popolamento pelagico ad entomostraci del

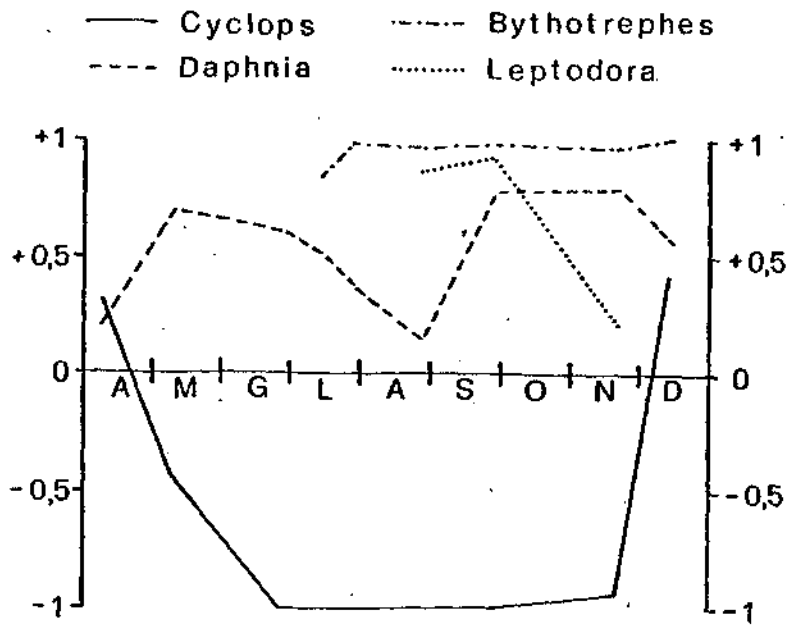


Fig. 3. - Andamento stagionale dell'indice di elettività di Ivlev calcolato per i principali organismi che intervengono nel regime alimentare del *Coregonus* sp.

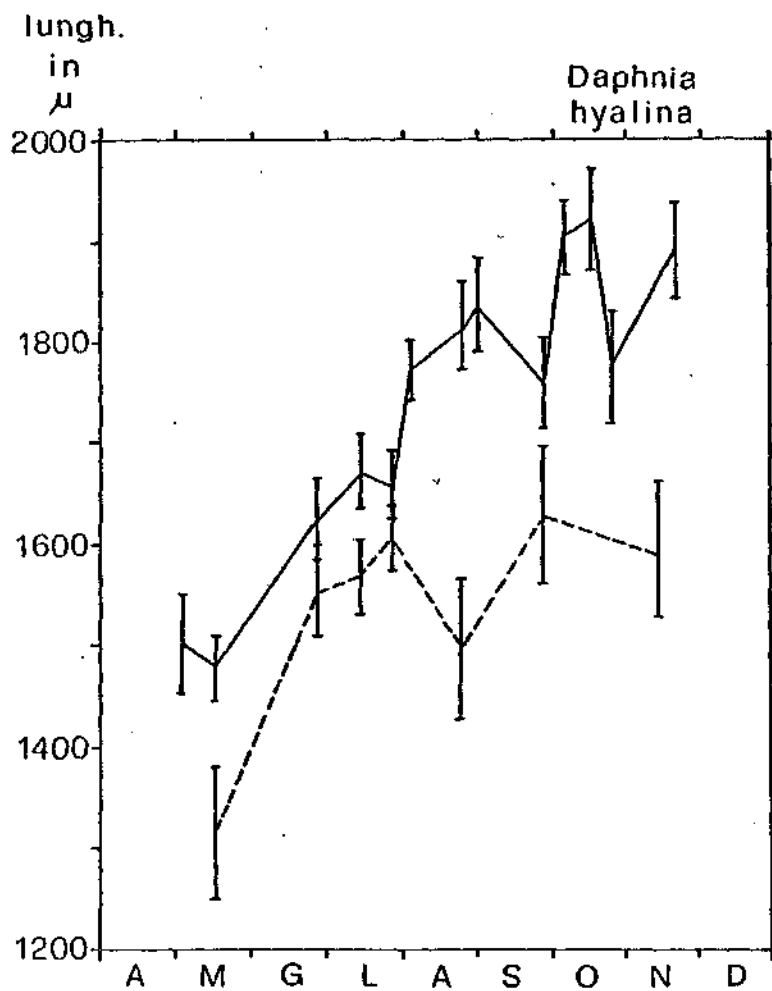


Fig. 4. - Confronto tra le dimensioni corporee (lunghezza media e relativo intervallo fiduciale) di *Daphnia hyalina* del contenuto gastrico di *Coregonus* sp. (—) e della popolazione naturale (- - -).

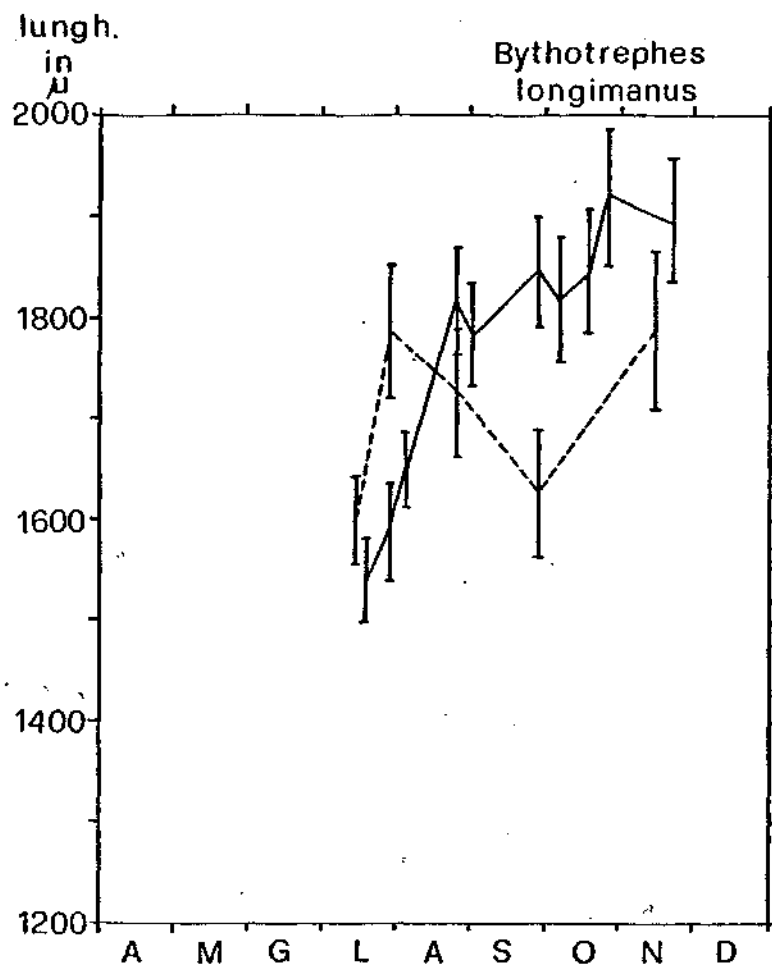


Fig. 5. - Confronto tra le dimensioni corporee (lunghezza media e relativo intervallo fiduciale) di *Bythotrephes longimanus* del contenuto gastrico di *Coregonus* sp. (—) e della popolazione naturale (---).

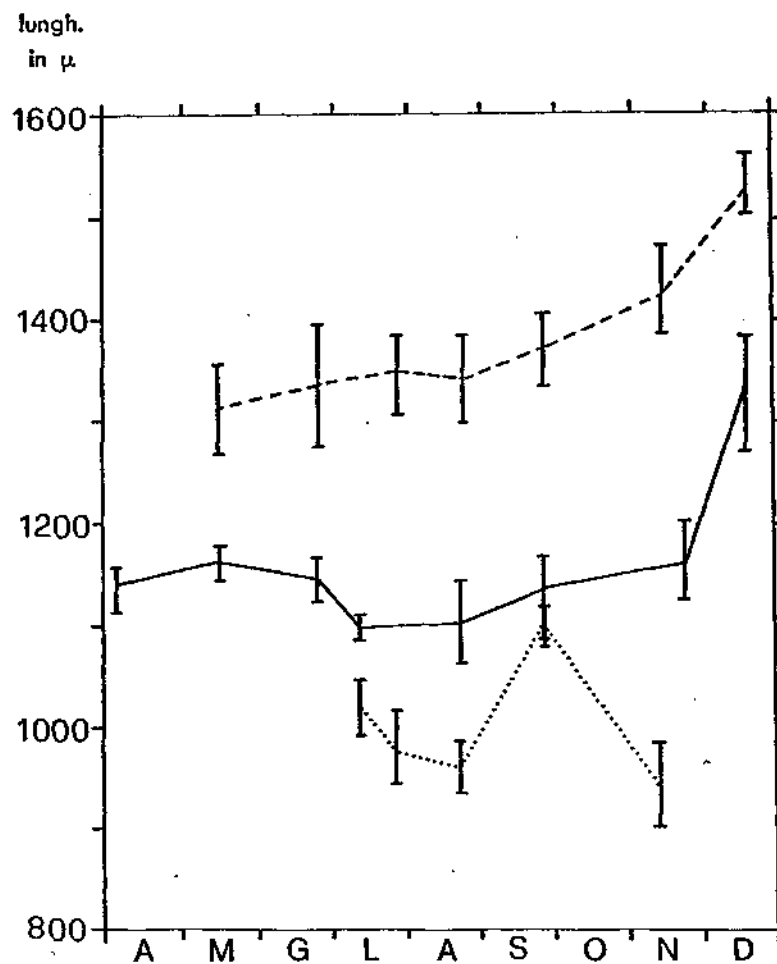


Fig. 6. - Lunghezza media e relativo intervallo fiduciale dei copepodi ciclopidi (---), diatomidi (—) e del cladocero *Diaphanosoma brachyurum* (.....) presenti nelle acque pelagiche del Lago Maggiore.

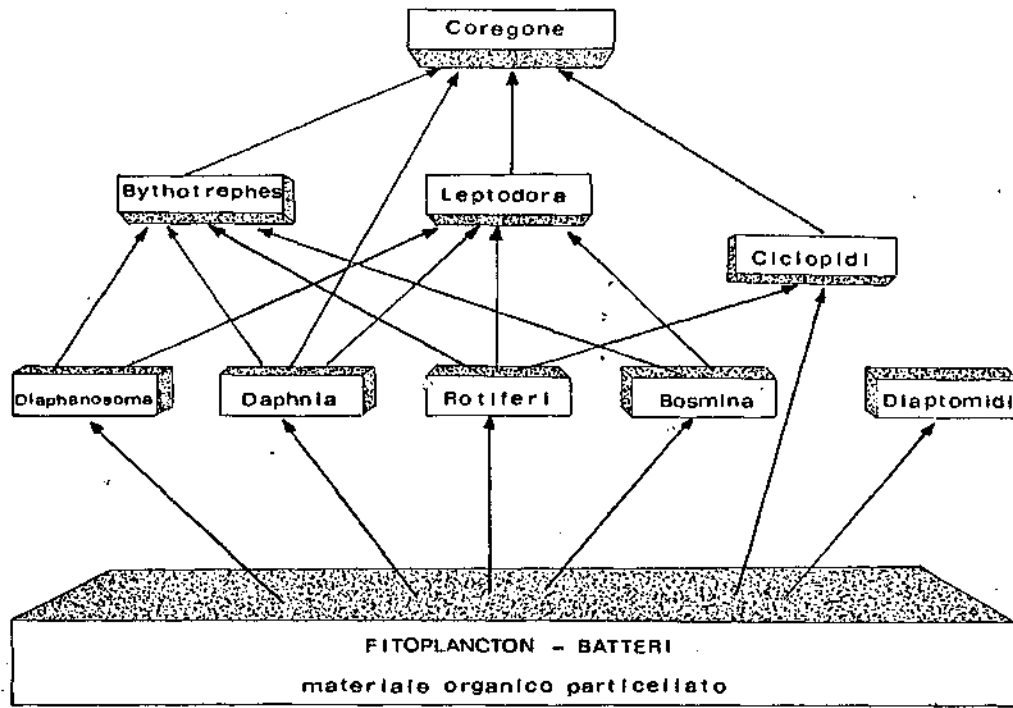


Fig. 7. - Rappresentazione schematica dei livelli trofici occupati dagli organismi coinvolti nella catena alimentare in esame.

Notice

Please note that these translations were produced to assist the scientific staff of the FBA (Freshwater Biological Association) in their research. These translations were done by scientific staff with relevant language skills and not by professional translators.