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Cladocera: Predators and prey

R. de Bernardi, G. Giussani & M. Manca
C.N.R. Istituto Italiano di Idrobiologia, 28048 Pallanza, Italy

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Abstract

Among the freshwater zooplankton community, Cladocera represent one of the most common elements of pelagic populations. Being almost exclusively filter feeders and algae users and, at the same time, the favourite prey of invertebrate and vertebrate predators, Cladocera represent the most important group in the plankton community of lakes as regards energy transfer along the food chain. Because of their short generation times and their high reproductive efficiency, predation by invertebrates, usually, has only a limited role in controlling their density. However, at high densities, invertebrate predators can provide an effective control of Cladocera populations. The intensive research on selective predation by vertebrates has demonstrated that this activity can be responsible, together with competitive interactions, for the dominance of different groups in the planktonic community: large Cladocera dominate when predation is low, Rotifera and small Crustacea dominate at high predation levels and high nannoplanktonic densities. These evidences on the role of vertebrate predation in structuring aquatic environments has greatly contributed to our better understanding of aquatic ecosystem functioning. In particular, it seems that the removal of large filter-feeding herbivorous Cladocera by zooplanktivorous fish can lead to worsening environmental conditions in eutrophicating lakes. In this respect, Cladocera appear to be the key group among zooplanktonic organisms, and their interactions the key factors in aquatic food chain management.

It is widely recognized that biotic interactions in freshwater ecosystems represent the most important factor determining species selection and the structure of biological communities. This is particularly true in the unstructured and partially uniform pelagic environment of lakes, where biotic interactions like competition and predation are extremely severe, because no refuge is offered by the environment.

Biotic interactions, therefore, exert an important selective pressure on pelagic organisms, which has induced a series of strategies to counteract or minimize the ill-effects of predation and competition, among which are: vertical migration (Cushing, 1955; Hardy, 1956; David, 1961; Wynne-Edwards, 1962; Narver, 1970; Dumont, 1972; McLaren, 1963 and 1974; Lane, 1975; Zaret & Suffern, 1976; Hairston, 1977; Buchanan & Haney, 1980; de Bernardi, 1981; Orcutt & Porter, 1983; Stich & Lampert, 1981, 1984; Weider, 1984), spatial segregation (Tappa, 1965; Dumont, 1972; Lane, 1975; de Bernardi & Soldavini, 1979; Weider, 1984), variations in size (Hrbáček, 1962; Hrbáčková-Esslová, 1963; Gilbert & Waage, 1967; Zaret, 1972a; Kerfoot, 1974; Dodson, 1974a; Pourriot, 1974; Zaret & Kerfoot, 1975; de Bernardi & Giussani, 1975; Langeland, 1978; Gophen, 1985), selection of less visible strains (Green, 1967, 1971; Zaret, 1972b; Zaret & Kerfoot, 1975), cyclomorphosis (Lauterborn, 1904; Brooks, 1946, 1964; Jacobs, 1961, 1964, 1965, 1966, 1980; Brooks, 1965; Hutchinson, 1967; Galbraith, 1967; Green, 1967; Brooks, 1968; Dodson, 1974b; Fedorenko, 1975; Kerfoot, 1970; O'Brien *et al.*, 1980; Black, 1980; Grant & Bayly, 1981; Wong, 1981;

Havel, 1985), and, finally, the induction of diapausing or resistant stages, such as cysts and ephippial eggs (Mellors, 1975).

Moreover, a further peculiarity of the pelagic environment is that primary producers (unicellular or colonial algae) are very small relative to the size of the planktonic herbivores. These herbivores in turn are much smaller than many of their own predators. Thus, because the pelagic environment is unstructured and uniform, and because pelagic predators are often much larger than their prey, the prey are completely open to predator attack. In addition, despite differences in the mechanisms of food collection (McMahon & Rigler, 1965; Hrbáček, 1977; Rubenstein & Koehl, 1977; Geller & Müller, 1981), all planktonic herbivores compete for particles in the same size range, about 1 to 15 μm (Brooks & Dodson, 1965; Geller & Müller, 1981).

However, we must take into account that in pelagic ecosystems, the relative importance of both predation and competition in structuring the zooplankton community may appear in different ways in different lakes in relation to the different environmental characteristics (both biotic and abiotic).

Among the freshwater zooplankton community, Cladocera represent one of the most common elements of pelagic populations. Usually they are more abundant in eutrophic, phytoplankton-rich waters, in which they may constitute the major component of phytophagous organisms (Hrbáček, 1977). In oligotrophic waters, their density is usually much less. With the exception of *Leptodora, Bythotrephes* and *Polyphemus* they are phytophagous covering a wide range of particle selection, competing with microfiltrators for smaller particles (1–20 μm) (Brooks & Dodson, 1965) and also being able to use larger food items (> 50 μm) (Burns, 1968; Gliwicz, 1969). Moreover, their body size ranges from 200–300 μm in mature chydorids to 7–8 mm in *Leptodora* and even more in the Cercopagidae. In this respect they may cover the whole size range of prey size taken by invertebrate and vertebrate predators. Being almost exclusively filter feeders and algae users and, at the same time, the favourite prey of vertebrate and invertebrate predators, Cladocera represent a key group in the plankton community of lakes as regards energy transfer along the food chain.

As a consequence of the high predation pressure both by vertebrates and invertebrates, they have developed a countering adaptation of parthenogenetic reproduction. This guarantees, through a high rate of reproduction, a rapid increase in population density, a ready adaptation to environmental fluctuations in food availability, and a certain ability to counterbalance mortality due to predation (Gadgil & Bossert, 1970).

As has been pointed out in many papers, the species of Cladocera are the major food supply of both vertebrate and invertebrate planktivorous predators.

However, the effects of predation by invertebrates or vertebrates on the dynamics of Cladocera populations, species selection, and evolution are very different. These differences derive mainly from the fact that vertebrates and invertebrates prey on different sizes. Whereas the electivity of vertebrates increases with prey size (Fig. 1a), invertebrates select smaller sized specimens (Fig. 1b). Thus, when both vertebrates and invertebrates prey upon a given species, the former select a size range corresponding to adult individuals, while the latter choose young, smaller sized specimens. Table 2 shows some of the most important features that characterize predation by vertebrates and invertebrates in pelagic freshwater ecosystems. Vertebrate predators are clearly much

Table 1. Main characteristics of the most important taxonomic groups of zooplankton (from de Bernardi, 1981).

	Rotifera	Cladocera	Copepoda
R max (1/day)	0.2–1.5	0.2–1.5	0.1–0.4
Typical adult body size (mm)	0.2–0.6	0.3–3.0	0.5–5.0
Largest species (mm)	1.5	5.0	14.0
Food size range (μm)	1–20	1–50	5–100
Filtering rate	very low	high	low
Susceptibility to vertebrate predators	very low	high	low
Susceptibility to invertebrate predators	high	moderate	moderate to high

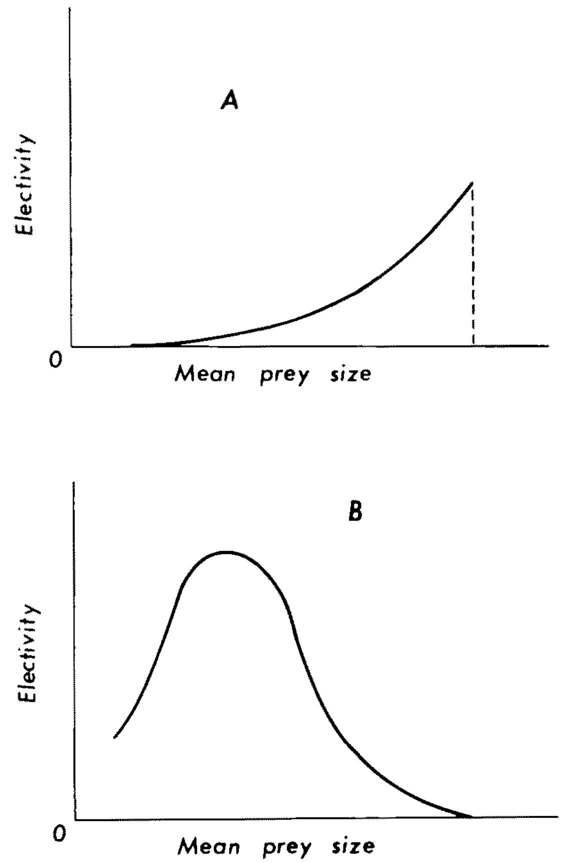


Fig. 1. An idealized representation of the effect of prey size on selection by vertebrate (A) and invertebrate (B) predators (from Zaret, 1980, redrawn).

more efficient in capturing prey, and therefore their impact on the dynamics of prey population is probably the most relevant.

The searching mode of preying by invertebrate predators is usually tactile or chemical, sometimes enhanced by receptors. This means that usually their search range is limited to a few millimeters, and the prey encounter can be considered casual (Fryer, 1957; Dodson, 1972; Fedorenko, 1975; Lewis, 1975; Strickler & Twombly, 1975; Pastorok, 1980, 1981; Riessen *et al.*, 1984; Kirk, 1985; Spitze, 1985; Gilbert & Stemberger, 1985).

Studies of predation by invertebrates upon planktonic Cladocera are usually concerned with rate of predation and the ways in which it is carried out (Anderson, 1981; Folt *et al.*, 1982). Table 3 reports some of the most interesting results obtained in this field.

The effect of this kind of predation at population level is shown in only a very few examples (Dodson, 1970; Confer, 1971; Sprules, 1972; Fedorenko, 1975; Langeland, 1981; Folt, 1985), and there are even fewer studies on the importance of invertebrate predators as a force structuring the Cladocera zooplankton community (Hall, 1964; Wright, 1965; Dodson, 1972; Duncan, 1975; de Bernardi & Giussani, 1975; Argentesi *et al.*, 1974; Ramcharan *et al.*, 1985).

Predation by invertebrates on Cladocera, because of the short generation times of the latter and

Table 2. Main characteristics of invertebrate and vertebrate predation on zooplankton (from de Bernardi, 1981).

Characteristics of predation	Predator type	
	Vertebrate	Invertebrate
searching mode	visual	tactile or chemical
search range	essentially unlimited	less than a few millimeters
prey size	very much smaller than the predator; large size strongly selected	usually smaller than the predator but increases with the predator size
prey selective	generally opportunistic; if sufficiently abundant, anything larger than above defined minimum size is consumed	unknown
prey escape	once seen, escape chances are low	probably depends on relative sizes of prey and predators and specific swimming speed
predator mobility relative to prey movement	considerably more mobile	somewhat greater than for prey
feeding rates of predators	high; may consume up to 10^4 zooplankton/day	easily saturated; predators usually consume less than their own weight per day

Table 3. Predation rates of some invertebrates.

Predator		Prey	Prey ind/l	Prey eaten per day	Reference
Cladocera					
Bythotrephes longimanus	(10 – 15 °C)	mixed zooplankton	–	9	Mordukhai-Boltovskaja 1960
Bythotrephes longimanus	(15 – 20 °C)	mixed zooplankton	–	27	Mordukhai-Boltovskaja 1960
Bythotrephes longimanus	(20 – 25 °C)	mixed zooplankton	–	25	Mordukhai-Boltovskaja 1960
Leptodora kindtii	(10 – 15 °C)	mixed zooplankton	–	16	Mordukhai-Boltovskaja 1960
Leptodora kindtii	(15 – 20 °C)	mixed zooplankton	–	25	Mordukhai-Boltovskaja 1960
Leptodora kindtii	(20 – 25 °C	mixed zooplankton	–	30	Mordukhai-Boltovskaja 1960
Insecta					
Chaoborus americanus IV instar		Daphnia rosea D. pulicaria Diaptomus sicilis	154	1.53	Anderson & Raasveldt 1974
Chaoborus americanus II instar		Diaphanosoma nauplii	–	20	Fedorenko 1975
Chaoborus borealis IV instar		Daphnia Aedes larvae	73	0.4	James & Smith 1958
Chaoborus flavicans IV instar		Copepods & Cladocera	8	8.8	Kajak & Ranke-Rybicka 1970
Chaoborus flavicans IV instar		Copepods & Cladocera	44	8.0	Kajak & Ranke-Rybicka 1970
Chaoborus flavicans IV instar		Daphnia pulex	99	4.4	Dodson 1970
Chaoborus trivittatus IV instar		Daphnia pulex	57	3.9	Dodson 1970
Chaoborus trivittatus III instar		Diaphanosoma	70	28	Fedorenko 1975
Chaoborus punctipennis		Holopedium	–	0.96	Allan 1973
Chaoborus punctipennis		Daphnia	–	2.13	Allan 1973
Chaoborus punctipennis		Bosmina	–	3.99	Allan 1973

their high reproductive efficiency, usually has only a limited role in controlling prey density. However, invertebrate predators at high densities can provide an effective control of prey populations.

The main invertebrate predators for zooplanktonic Cladocera are such planktonic species as adult cyclopoid copepods, carnivorous Cladocera, and, among insects, meropelagic organisms such as *Chaoborus* and midge larvae.

The most efficient invertebrate predators of Cladocera are the carnivorous *Leptodora* and *Bythotrephes* (which can capture up to 30 prey/day) and *Chaoborus* larvae (Monakov, 1972). All species of herbivorous Cladocera may become a prey for invertebrates, even the largest species. In the latter case, young (= small) individuals will be selected positively. For small species, such as chydorids and bosminids, invertebrate predation can also be for adults. Some authors have indicated that invertebrate predation on small organisms, together with competition for food, are the prevailing factors responsible for the dominance of large Cladocera when the predation pressure by vertebrates is low (Hrbáček, 1962; Hrbáčková-Esslová, 1963; Hall, 1964; Brooks & Dodson, 1965; Stenson, 1972; de Bernardi & Giussani, 1975; Andersson *et al.*, 1978; Langeland, 1978; Gliwicz *et al.*, 1981).

The mechanisms underlying these processes have not been fully evaluated. Nevertheless, it is clear that, while vertebrate predation has an important effect on zooplankton community structure and dynamics, the role of invertebrate predation is not inconsiderable, despite the fact that available information relevant to this second process is much sketchier (Bossone & Tonolli, 1954; Wright, 1965; McQueen, 1969; Cummins *et al.*, 1969; Anderson, 1970; Anderson & Raasvelt, 1974; de Bernardi, 1974; de Bernardi & Giussani, 1975; de Bernardi & Canali, 1975; Fedorenko, 1975; Threlkeld *et al.*, 1980).

Bossone & Tonolli (1954) provide a particularly good example of how invertebrate predation can influence zooplankton community structure. They found that the coexistence of two herbivorous diaptomids (*Arctodiaptomus bacillifer* and *Acanthodiaptomus denticornis*) in a high alpine lake in Northern Italy (Lago di Monscera, altitude 2071 m) depended upon the predation by *Heterocope saliens* on the former. Even if this example refers only to copepods, there is no reason to suppose that such kind of effect does not occur also for Cladocera. An appropriate example could be

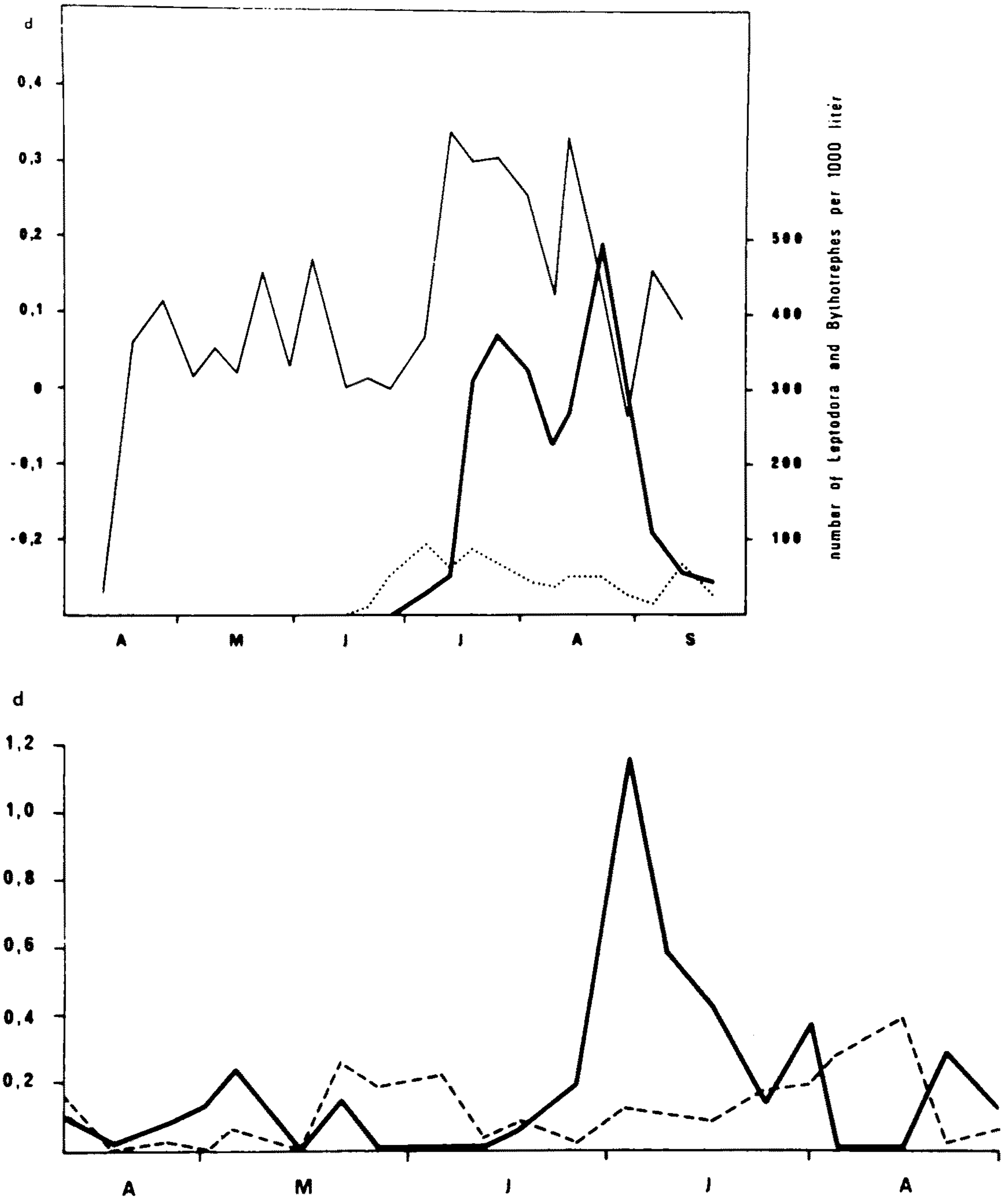


Fig. 2. The annual catch of whitefish and the densities of *Daphnia hyalina* (———), *Leptodora kindtii* (...) and *Bythotrephes longimanus* (– –) in 1972 and 1973 (from de Bernardi & Giussani 1975).

the role of *Leptodora* predation on the competition between *Daphnia* and *Diaphanosoma* in Lago Maggiore, where the *Diaphanosoma* population can increase in density only when *Daphnia* declines from predation by *Leptodora* and *Bythotrephes* (de Bernardi & Canali, 1975). From these studies it emerged also that, following a decline of the 'bondella' whitefish in 1973, there was a marked increase in the populations of its prey, namely the herbivore *Daphnia hyalina* and the two predator Cladocera, *Bythotrephes longimanus* and *Leptodora kindtii* (Fig. 2). The daphniid population showed a substantial spring increase in density, followed by an equally rapid decline in early summer, when the populations of these two invertebrate predators increase. Detailed analysis of the population dynamics of *Daphnia* (de Bernardi, 1974) by a compartmental model for different age classes (Argentesi *et al.*, 1974) showed that the collapse of the *Daphnia* population was due to an increase in the juvenile mortality rate (Fig. 3), reflecting predation by *Leptodora* and *Bythotrephes*, which select prey in the size range of young *Daphnia hyalina* (Mordukhai-Boltovskaya, 1958).

These experimental results have been validated by a statistical analysis that confirms the highly significant correlation between the death rate of young *Daphnia* and the fecundity rate of *Leptodora*, as shown in Fig. 4.

Similar evidence of the effect of *Leptodora* predation on the *Daphnia* population has been observed by Duncan (1975) in London Reservoir, as shown in Fig. 5.

Further evidence of invertebrate predation balancing competition is presented by Allan (1973), who found that *Chaoborus* predation on *Daphnia* allows the coexistence of *Holopedium*. The inferior competitor *Holopedium* can survive, because its gelatinous cover protects the young against predation.

Chaoborus predation on Cladocera may result in contrasting effects; for example, Neill (quoted in Pastorok, 1980) found that *Daphnia rosea* populations were twice as abundant in the absence of

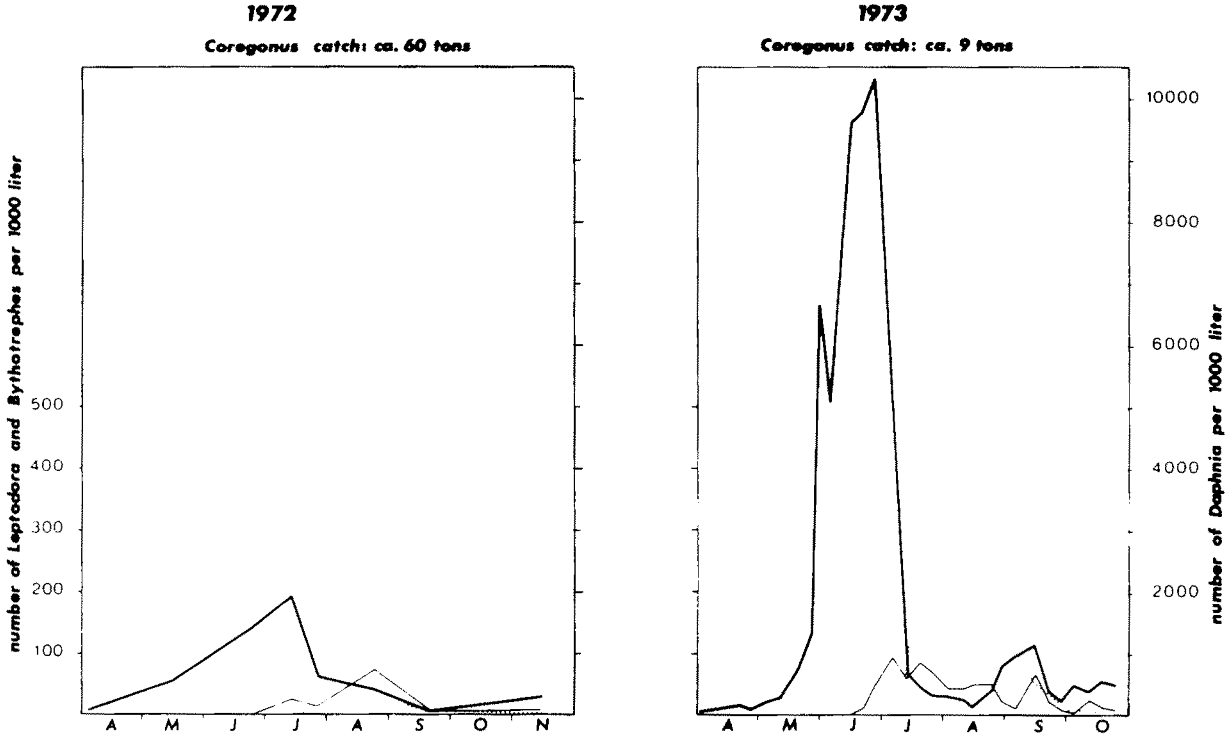


Fig. 3. Upper: the densities of *Leptodora kindtii* (———) and *Bythotrephes longimanus* (...) and the instantaneous mortality (d) (– –) of the entire daphniid population in Lago Maggiore. Lower: the instantaneous mortalities of young (———) and adult (– – – –) *Daphnia hyalina* (from de Bernardi & Giussani, 1975).

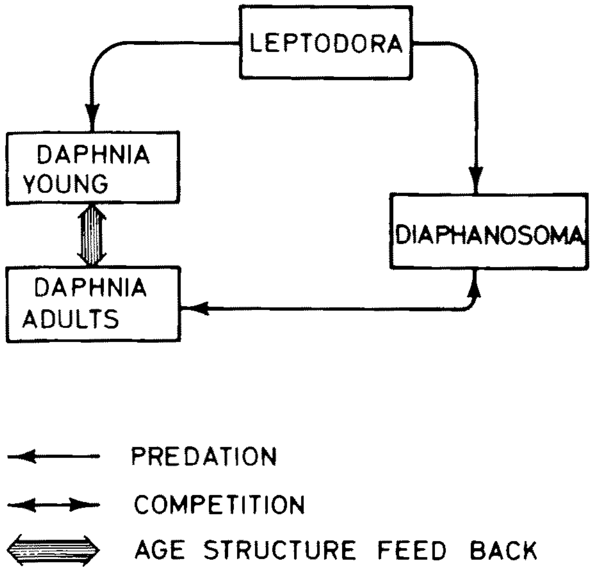


Fig. 4. Trophic relationships among pelagic Cladocera in Lago Maggiore tested by ARIMA Models (from Argentesi & de Bernardi, 1978).

Chaoborus. Smyly (1976), after the experimental removal of *Chaoborus*, documented a shift in dominance relations among the zooplankton, with no species invading or becoming extinct. On the other hand, Lynch (1977) found that *Chaoborus* excluded *Ceriodaphnia* from experimental vessels. In contrast, large rapidly growing Cladocera, like *D. pulex*, *D. pulicaria*, and *Simocephalus vetulus*, may coexist with *Chaoborus* by exploiting a strategy of escape in size (Dodson, 1974a; Paine, 1974; Kerfoot & Pastorok, 1978; Zaret, 1978; Pastorok, 1978).

More data are available about the rates of invertebrate predation on Cladocera (Table 3). However, it must be stressed that, despite the great number of papers dealing with predation rates by invertebrates, up to now it has still not been possible to evaluate the weight of invertebrate predation on lake ecosystem structure and functioning. The measured levels of invertebrate predation can range from 10% (Brandl & Fernando, 1981) to 90% (Dodson, 1972). However, even at the highest levels, invertebrate predation alone never seems to determine the disappearance of a species. In particular, Dodson (1972) reported an extreme case in which a population of *Daphnia rosea* survived despite such heavy predation by *Chaoborus* that the instantaneous mortality rate of the cladoceran reached 90% per day. Such low effectiveness of invertebrate predators may be explained partially by the results recently obtained from laboratory experiments in which artificial size selective predation was exerted on *Daphnia* populations. In particular, in these experiments the dynamics of the density of seven populations of *Daphnia obtusa* submitted to different levels of predation were analyzed over a period of about one year. The experimental design provided information on three different levels of predation (30%, 60% and 90%) every two days, exerted separately on young, adults, and at random. The main results are reported in Fig. 6, which demonstrates that at all levels of predation experimentally induced, predation on the immature individuals produced less damage on the population. When predation is exerted on both young and adults, density drops very quickly, thus confirming in the laboratory evidence obtained in natural environments, where the disappearance of a species has been observed when both kinds of predation were active (Zaret & Paine, 1973; Richards *et al.*, 1975; Goldman *et al.*, 1979; Gophen, 1979).

A further explanation of the results may also be attributed to the biological characteristics of these organisms. The adult females carry their eggs in the brood pouch and, under experimental conditions, each female once mature produces eggs in each instar almost until death. The consequence is that predation on adult females works as a simultaneous predation on eggs and reduces the recruitment of new individuals into the population.

However, the fact that these results have been obtained under laboratory conditions must be kept in mind, because in natural environments predation levels are never constant, and, in addition, trophic relationships in a lacustrine community can never be reduced to a simple binary connection.

However, these experiments also indicate that predation by vertebrates can have a potentially high ill-effect on Cladocera species.

In Fig. 1 we presented the electivity of vertebrate predation in respect to prey size. The general rule is that electivity increases with size of prey. This is true both for obligate and facultative planktivorous species (Brooks & Dodson, 1965; Galbraith, 1967; Giussani, 1974; Hall *et al.*, 1976; O'Brien *et al.*, 1976; Langeland, 1982; Gophen, 1985).

Starting from papers by Hrbáček (1960) and Hrbáček *et al.* (1960, 1961), and Brooks & Dodson

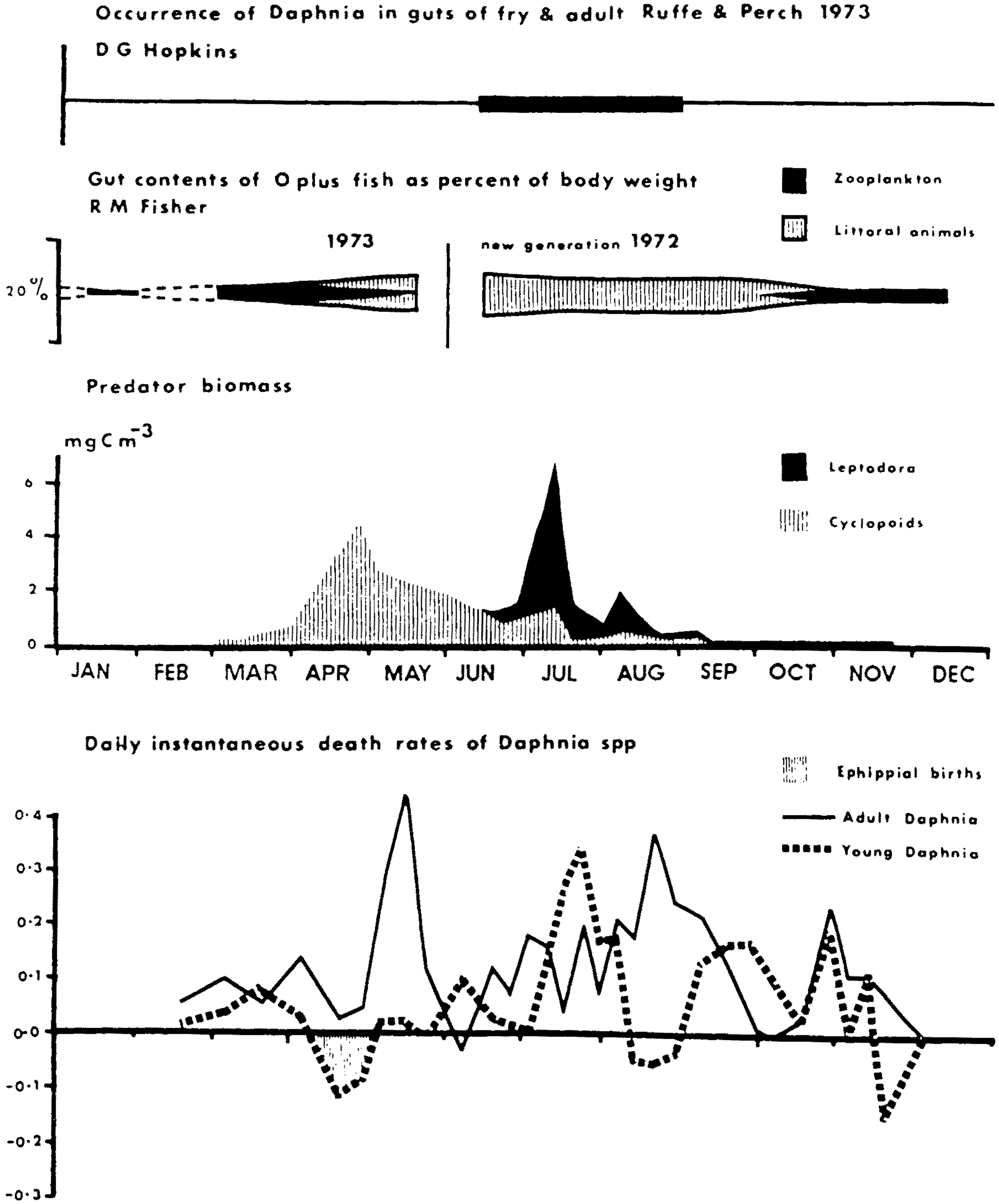


Fig. 5. Daily instantaneous death rates of young and adult daphniids in Queen Elisabeth II Reservoir in 1972, compared with the seasonal pattern of invertebrate predator biomass and the presence of zooplankton in the guts of 0^{+} or adult fish (from Duncan, 1975, redrawn).

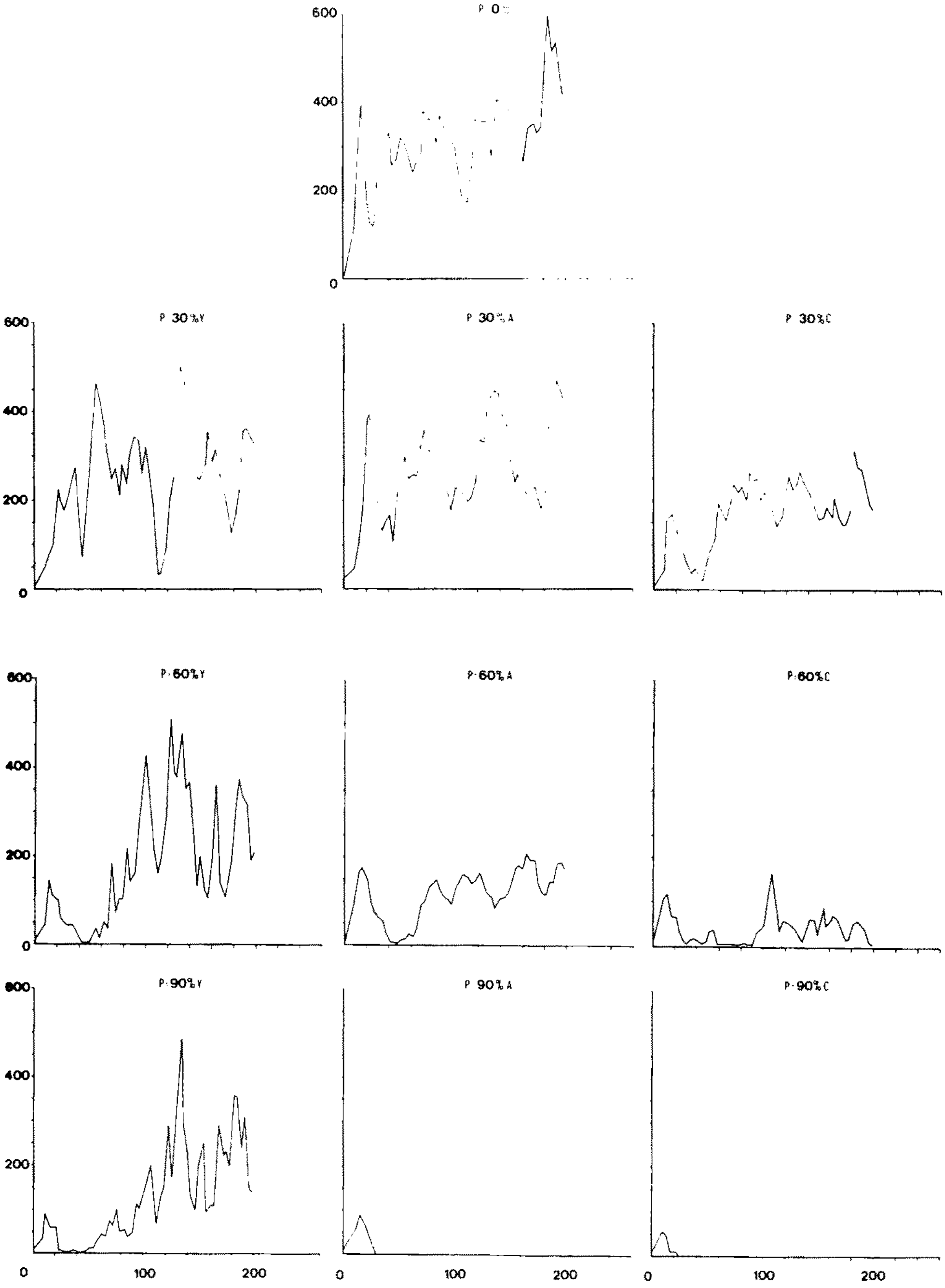


Fig. 6. Effects of three different levels of selective predation (30%, 60% and 90%) on the dynamics of experimental populations of *Daphnia obtusa* (Y = selective predation on young; A = selective predation on adults; C = random predation) (from de Bernardi, 1981).

(1965), an intensive research activity on selective predation by vertebrates (mainly fish and salamanders) has been developed. From these studies, two main theories have emerged, largely overlapping, the first, focusing attention on size selection (Hrbáček, 1962; Brooks & Dodson, 1965; Dodson, 1974a; Werner & Hall, 1974; Taylor, 1980) and the second, stressing the importance of visibility of prey (Fox, 1948; Boulet, 1958; Braum, 1963; Greze, 1963; Hemmings, 1966; Wawrik, 1966; Brooks, 1968; Hester, 1968; McNaught, 1975; Zaret, 1972b; Nilsson & Pejler, 1973; Ware, 1973; Dodson, 1974b; Mellors, 1975; Zaret & Kerfoot, 1975; Kring & O'Brien, 1976; O'Brien *et al.*, 1976; Eggers, 1977; Kerfoot, 1980; Stenson, 1980; Zaret & Kerfoot, 1980).

However, it must be noted that in many cases large organisms also present a greater visibility, and hence this large amount of work seems to confirm, at least partially, Brooks & Dodson's size selective hypothesis (1965).

In particular, this body of research has shown that predation together with competitive interactions is responsible for the dominance of different groups in the planktonic community: large Cladocera dominate when predation is low, Rotifera and small Crustacea dominate at high predation levels and high nannoplanktonic densities (Hrbáček, 1962, 1977; Brooks & Dodson, 1965); organisms with a large spectrum of sizes can coexist when selective predation is moderate, thus confirming the fact that predation represents a mechanism that maintains disequilibrium among competing species (Hrbáček, 1962; Paine, 1966; Dodson, 1970; Dumont, 1972; Allan, 1974; Lane, 1975; Lewis, 1980).

Since the well-known example presented by Brooks & Dodson (1965) on Crystal Lake, particularly impressive evidence has been presented by Langeland (1982) through the comparison of species and size composition of zooplankton from five lakes characterized by different fish predation pressure (Fig. 7).

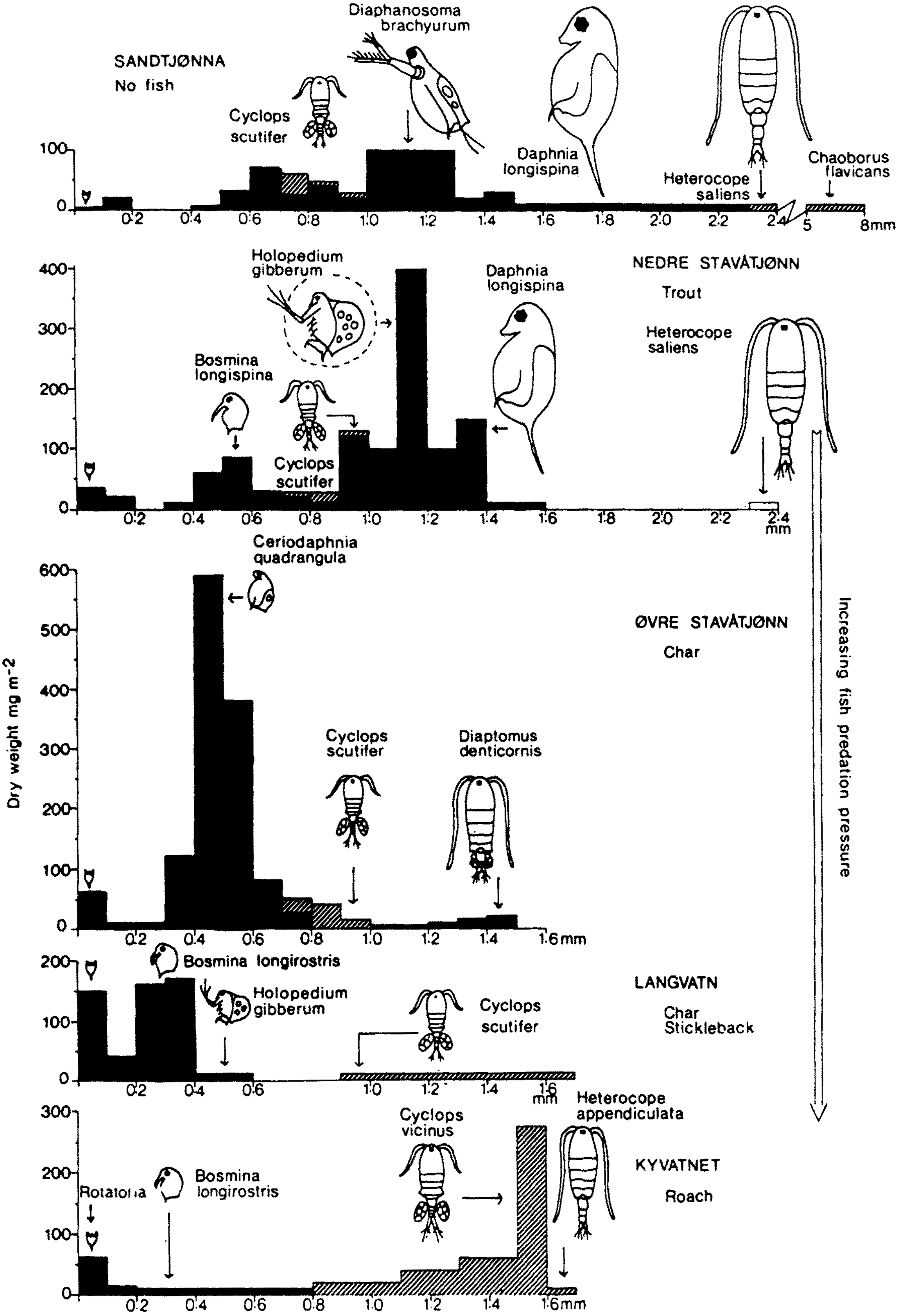
Other than size and visibility selection, vertebrate predation presents a series of characteristics that determine its highly damaging effect on Cladocera species (Table 2). Once seen, the prey has no chance of escaping. Moreover, each single predator, conducting an active search for prey in a large area, is able to consume a very large number of prey/day (up to 10^4 organisms/day).

A few representative examples from the great number of papers on this subject in the last 20 years can illustrate easily the importance of vertebrate predation on Cladocera populations. In the Lago Maggiore system it has been demonstrated that among the zooplanktonic species, *Leptodora, Bythotrephes* and *Daphnia* are the most electively selected by planktivorous fish, and that among all of them, electivity increases with size (Giussani, 1974) (Fig. 8).

The results obtained in this research also indicate that a size-specific selectivity exists even within the same species (de Bernardi & Giussani, 1975) (Fig. 9).

Galbraith (1967) studied the recovery and development of the zooplankton community of Sporley Lake after the original fish and zooplankton had been eliminated with toxaphene. When the zooplankton reappeared, it included two *Daphnia* species, one large (*D. pulex*) and the other smaller (*D. retrocurva*). The subsequent introduction of *Salmo gairdneri* and *Perca flavescens* into the lake led to the local extinction of larger *D. pulex* and the increase in number of tiny *D. retrocurva*. Schindler & Comita (1972) obtained similar results in a Canadian pond when prolonged complete deoxygenation destroyed the fish. During the following spring, tiny *Daphnia parvula*, which had been present before the fish kill, reappeared. Soon afterwards, the larger *D. pulex*, which had not been found previously, appeared and eliminated *D. parvula* from the pond. The elimination of fish predation thus shows that fish influence the Cladocera community both directly by killing the larger individuals and indirectly by altering competitive forces within the herbivorous Cladocera community. Analogous findings have been reported from the rocky intertidal zone (Paine, 1974) and from prairies (Harper, 1969).

Still more evidence from zooplankton communities is provided by observations on Lago d'Annone (Northern Italy) (de Bernardi & Giussani, 1978). This lake is divided into east and west basins, both of which normally maintain a substantial population of bleak (*Alburnus alburnus alborella*), which is by far the most important planktivorous fish in the lake. In the summer of 1975, within a few days almost the entire bleak population (about 50 tons) in the east basin was wiped out because of a fungal


SANDTJØNNA
No fish
Cyclops scutifer
Diaphanosoma brachyurum
Daphnia longispina
Heterocope saliens
Chaoborus flavicans
100
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6
1·8
2·0
2·2
2·4
5
8mm
NEDRE STAVÅTJØNN
Trout
Holopedium gibberum
Bosmina longispina
Cyclops scutifer
Daphnia longispina
Heterocope saliens
400
300
200
100
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6
1·8
2·0
2·2
2·4 mm
ØVRE STAVÅTJØNN
Char
Ceriodaphnia quadrangula
Cyclops scutifer
Diaptomus denticornis
Dry weight mg m^{-2}
600
500
400
300
200
100
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6mm
Increasing fish predation pressure
LANGVATN
Char
Stickleback
Bosmina longirostris
Holopedium gibberum
Cyclops scutifer
200
100
0
0·2
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1·6 mm
KYVATNET
Roach
Rotatoria
Bosmina longirostris
Cyclops vicinus
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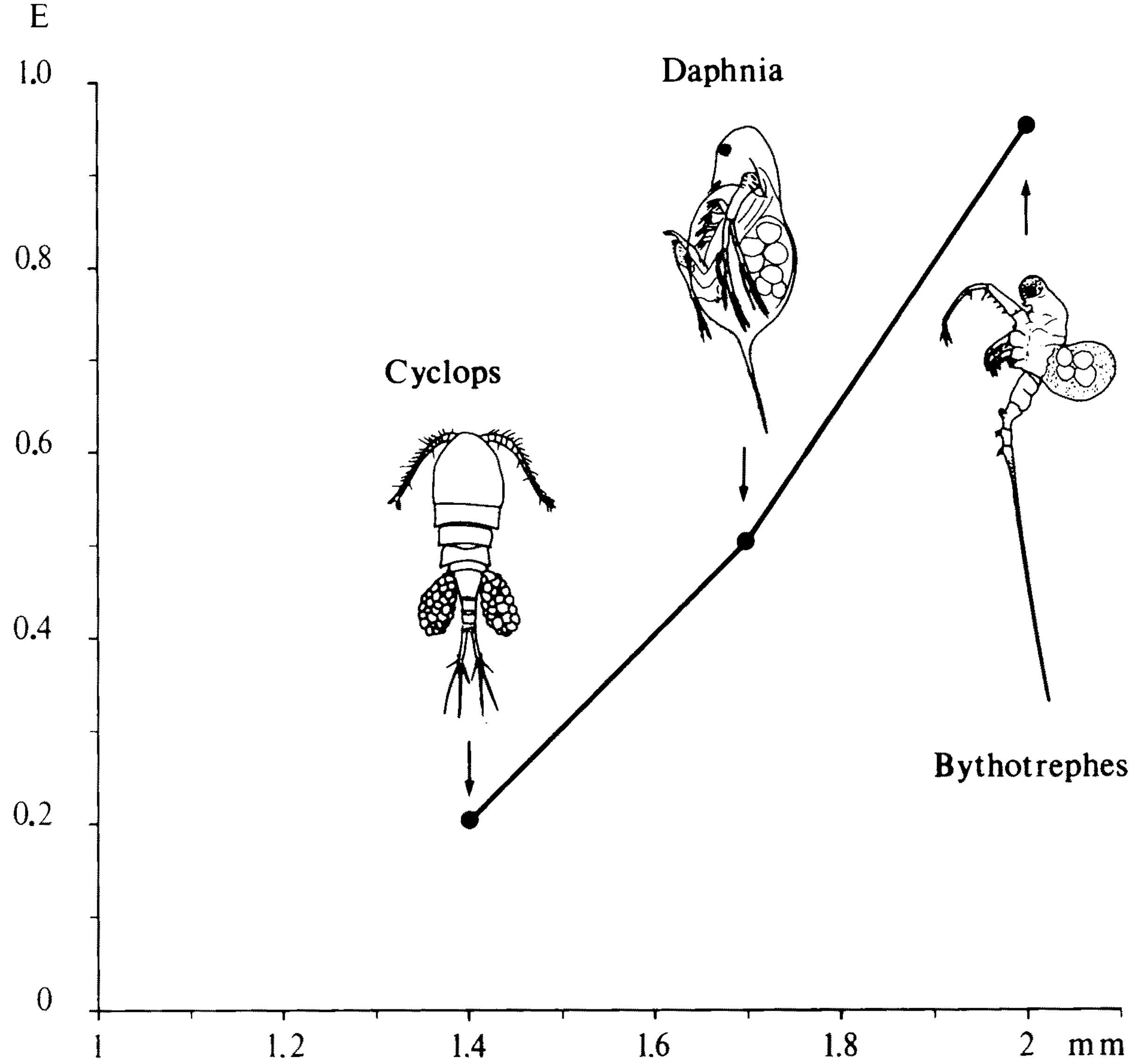

Fig. 8. The effect of length (mm) of 3 species of potential prey on whitefish prey preference in Lago Maggiore (data elaborated from Giussani, 1974).

Fig. 7. Species composition and the structure of the zooplankton community in lakes with different predation pressure (from Langeland, 1982, redrawn).

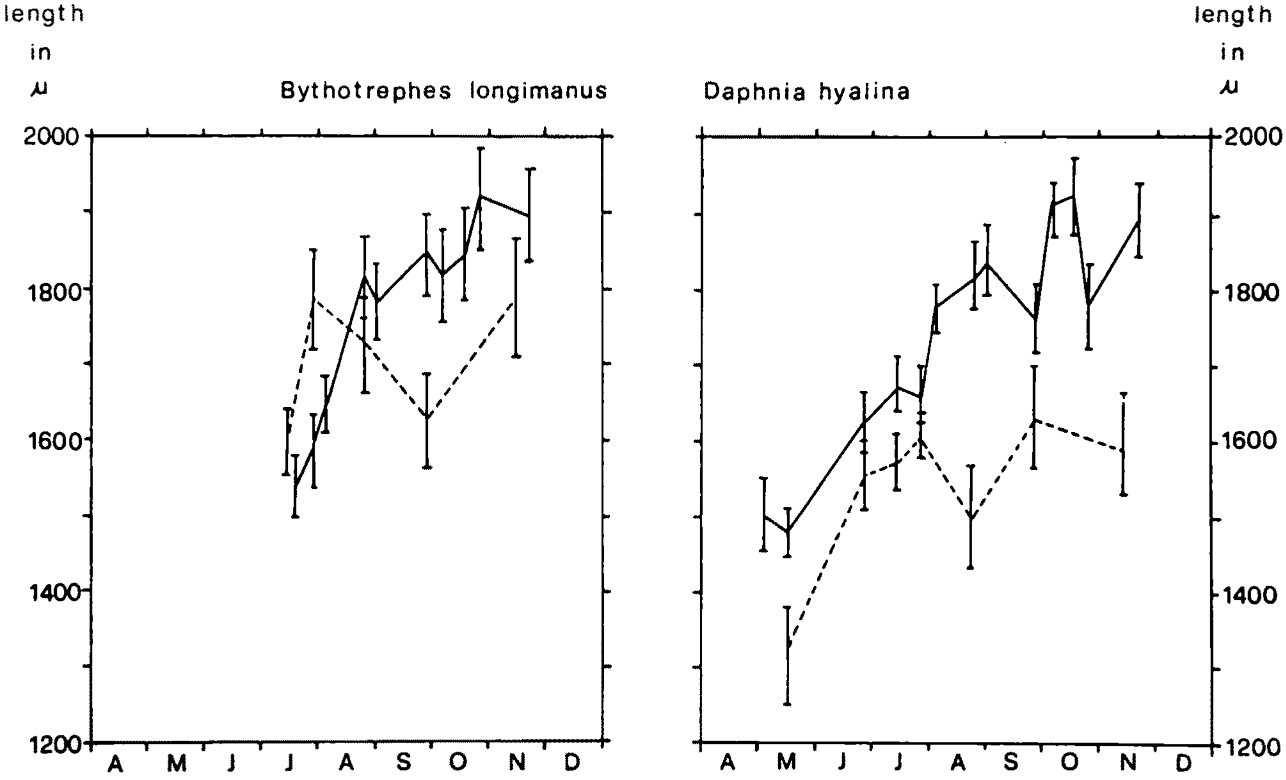

Fig. 9. Average sizes and confidence limits (5%) for *Daphnia hyalina* and *Bythotrephes longimanus* in the Lago Maggiore (– – – –) and in the stomach content (– –) of *Coregonus* sp. (from de Bernardi & Giussani, 1975).

gill infection, while in the west basin the bleak population was almost untouched. The effects on the Cladocera community were very clear (Fig. 10): in the east basin, where the mortality had occurred, there was a marked increase in *Daphnia hyalina*, and a corresponding decrease in the population density of tiny *Bosmina*. The same study also showed the role of natural selection in reducing the effects of size-selective predation by the bleak on larger *Daphnia* (Fig. 11). For some years prior to the die-off, the bleak population had increased yearly, with a consequent reduction in the maximum size of *Daphnia* in the east basin; these *Daphnia* reached maturity at the small size of 630 µm. Just 15 days after the fish mortality, the minimum size at maturity had become 1000 µm, as in the west basin. It seems that intense predation by the bleak favoured small, early maturing daphniid strains, which after the disappearance of the bleak were competitively eliminated by larger strains.

Similar findings emerged from research carried out by Langeland (1978) showing the decline in mean body length of adults of both *D. galeata* and *Holopedium gibberum* in relation to increasing fish predation pressure (Fig. 12).

Hrbáček & Hrbáčkova (1960) found that strains of the same species of *Daphnia* from lakes and ponds with different fish stock presented differences in body-length increase in laboratory experiments with high food availability. In particular, strains from environments with low or absent fish predation pressure, had a larger increase than species and strains collected in water bodies with high fish predation. Moreover, they also found that smaller females produced smaller eggs, resulting in smaller newborn.

The different prey selectivity and in more general terms, the different features that characterize predation by vertebrates (see Table 2) may be responsible for the evolutionary divergence of closely related prey species. For example, de Bernardi & Manca (1982) and Manca & de Bernardi (in press) have

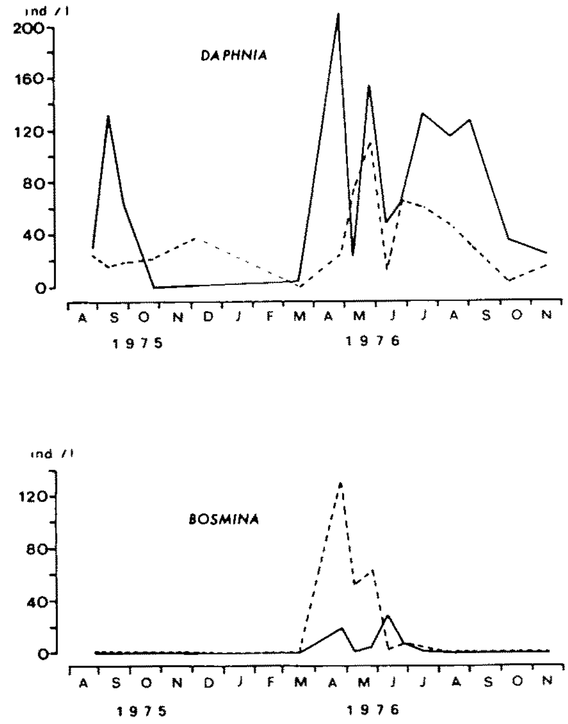

Fig. 10. The seasonal development of populations of *Daphnia* and *Bosmina* in the eastern (– –) and western (– – –) basins of Lago di Annone after a fish kill in 1975 in eastern basin (from de Bernardi, 1981).

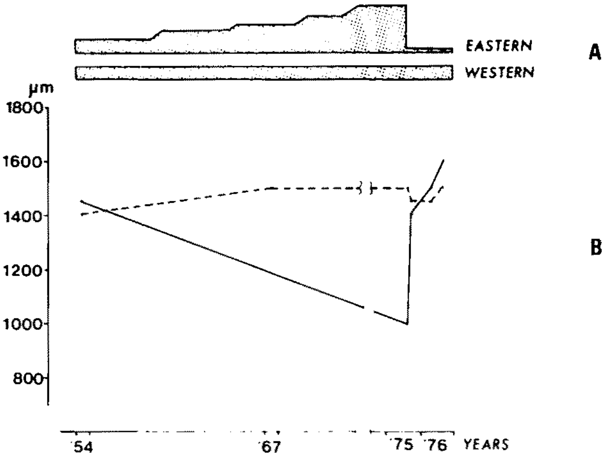

Fig. 11. An estimate of the density of the planktivorous fish *Alburnus alburnus alborella* (A), and the maximum length of *Daphnia hyalina* (B) in the eastern (– –) and western (– – – –) basins of Lago di Annone (from de Bernardi, 1981).

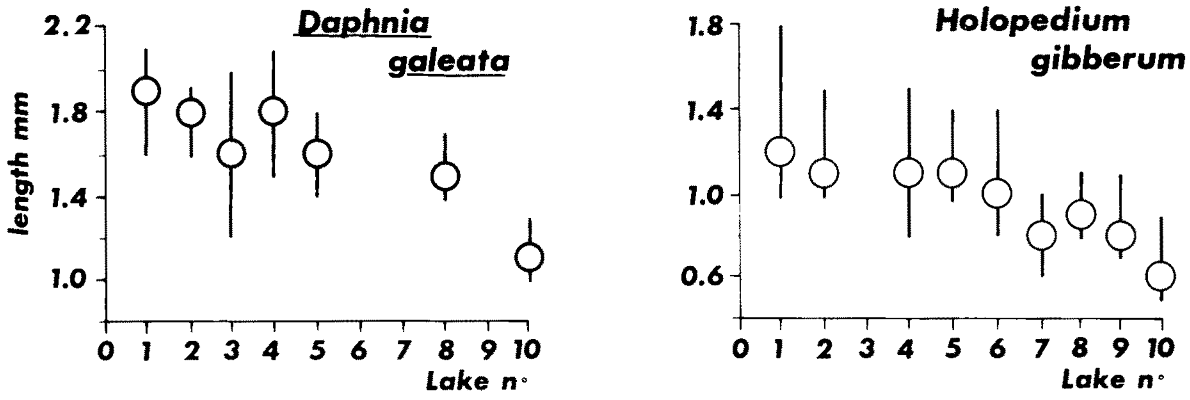

Fig. 12. Mean length (min. and max. indicated by bars) of adult *Daphnia galeata* and *Holopedium gibberum* during July–August in lakes with increasing predation pressure by arctic char (*Salvelinus alpinus*) from lake no. 1 to lake no. 10 (from Langeland, 1978).

shown that the two filter-feeders *D. obtusa* and *S. vetulus* have developed a strategy of food utilization and energy partitioning between reproduction and somatic growth as a result of coevolution with their dominant predators. When food is lowered, the free swimming *D. obtusa*, which is more subject to vertebrate predators, consumes the available energy to maintain a high rate of egg production, with a consequent lowering of somatic growth. *S. vetulus*, which is preyed upon more intensively by invertebrates, presents an inverse strategy.

The large body of evidence accumulated during the last twenty years on the role of vertebrate predation in structuring aquatic environments has greatly contributed to our better understanding of aquatic ecosystem functioning. It now appears evident that the removal of large filter-feeding herbivorous Cladocera by zooplanktivorous fish can lead to worsening environmental conditions in eutrophicating lakes.

In effect, large Cladocera are also the most efficient in removing algae from lake water. For that reason, an enhancement of their population through an effective control of the density of zooplanktivorous fish can increase water transparency through an increase in Cladocera filtering activity. This kind of intervention, initiated in the pioneering studies of Hrbáček & co-workers (1960, 1961), and called biomanipulation for the first time by Shapiro *et al.* (1975), shows fairly well how theoretical studies can produce results far beyond their immediate interest, and lead to the possibility of a direct management of ecosystem structures. In this respect, Cladocera appear to be the key group among zooplankton organisms, and their interactions the key factors in aquatic food chain management. If we look at the results obtained in the past on Cladocera population dynamics in the light of this new approach, we can see clearly the role of selective predation on the Cladocera population.

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