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*Submitted: 30 November 1992*
*Accepted: 29 June 1993*
*Amended: 11 August 1993*

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*Limnol. Oceanogr.*, 39(2), 1994, 395–403
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# The size ratio between planktonic predators and their prey

*Abstract*—Size selectivity spectra of 28 planktonic predators from 18 studies in the literature are compared. The linear size ratio between predators and their optimal prey is 1 : 1 for a dinoflagellate, 3 : 1 for other flagellates, 8 : 1 for ciliates, 18 : 1 for rotifers and copepods, and ~50 : 1 for cladocerans and meroplankton larvae. These size ratios seem consistent within groups, and their validity is supported by quantitative information from the literature. However, a difference between filter feeders and raptorial-interception feeders, preferring relatively smaller and larger prey respectively, is evident across the taxonomic groups. A classification of planktonic predators into functional groups is therefore crucial for the construction of models of pelagic food webs.

The pathways for flow of organic matter in pelagic food webs are to a wide extent determined by the food selectivity of the pelagic predators. Several criteria may be involved in food selection, including prey size, motility, surface characteristics, biochemical composition, electrostatic forces, etc. (e.g. Poulet and Marsot 1978; Robinson 1983; Gilbert and Bogdan 1984; Van Alstyne 1986). Among these criteria, prey size is generally believed to play a major role, and usually a fixed size ratio of 10 between predator and prey is assumed (Sheldon et al. 1977; Conover and Huntley 1980; Azam et al. 1983). This assumption is in accord with the classification of plankton into logarithmic size fractions (pico, nano, micro, meso, and macro, sensu Sieburth et al. 1978), and it has facilitated integrative trophodynamic studies of pelagic environments above the population level. This assumption has also been instrumental in the formulation of models of pelagic ecosystems for theoretical and steady state considerations (e.g. Kerr 1974; Azam et al. 1983) as well as for the formulation of carbon budgets and dynamic simulation (e.g. Riemann et al. 1990; Maloney and Field 1991). Longhurst (1990) asked whether there is a generalized prey : predator ratio within protists, invertebrates, fish, and cetaceans and found a standard deviation of 2.5 times the mean predator : prey ratio. He concluded that including more data only increases scatter around the regression line, and therefore that it is difficult to generalize ratios even within groups that appear to be relatively homogeneous.

In this note we re-evaluate the assumption of a fixed size ratio between pelagic predators and their prey on the basis of data now available in the literature. Data were selected from laboratory studies where size selectivity has been assessed with one prey size at a time at a constant initial volume fraction and from in situ studies with tracer particles added to the natural prey composition. In some of these studies selectivity was expressed as an Ivlev electivity index (Ivlev 1955). The studies cover pelagic predators of 5–1,000 μm (nano-, micro-, and mesozooplankton) from freshwater as well as marine environments.

Size selectivity is usually expressed as a ratio of ingestion rates of two or more size classes

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*Acknowledgments*
We are indebted to T. Fenchel and T. Kiørboe for comments on the manuscript.

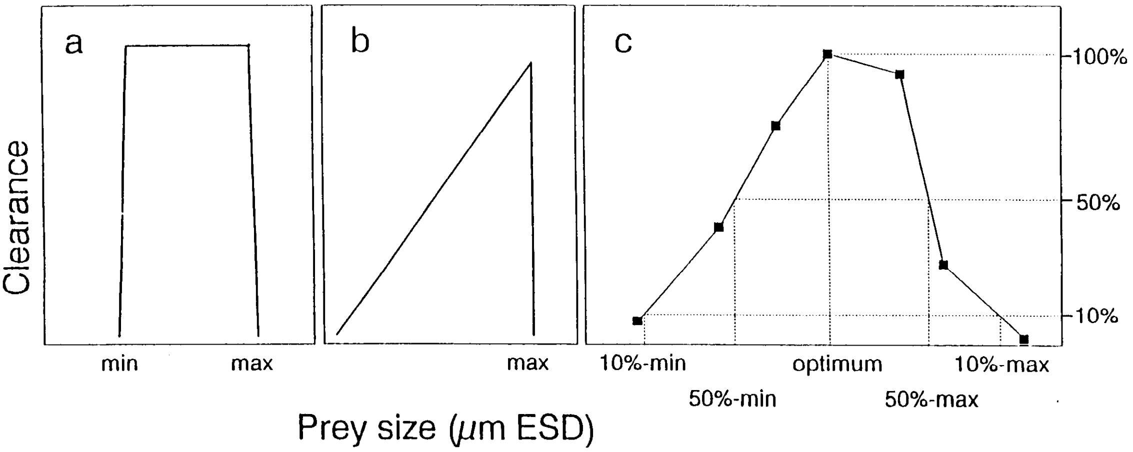

Fig. 1. Size selectivity spectra as expressed by maximum clearance vs. prey size. [a.] Hypothetical spectrum for an idealized filtrator with uniform filter porosity. [b.] Hypothetical spectrum for an idealized predator feeding by direct interception. [c.] Example of a spectrum from the literature illustrating the definition of optimum, 50%-min and -max, and 10%-min and -max prey sizes.

of prey normalized against their availabilities. Because clearance measures the ratio of ingestion to prey availability (density), size selectivity may also be expressed by maximum clearance (i.e. clearance at low prey density) for different prey sizes. The size range of particles that can be ingested by a pelagic predator is limited by the morphology of its feeding apparatus (e.g. maximum prey size may be set by the width of the cytostome, mouth or esophagous, and specifically by the carapace slit in cladocerans or by the distance between bands in rotifers and double-band larvae: Gliwicz 1977; Peters 1984; Rassoulzadegan et al. 1984; B. Hansen 1991). For filtrators, a minimum prey size is set by the mesh size of the filtering apparatus (Fig. 1a). Within these structural limits, a functional size selectivity often occurs. For predators feeding by direct interception, theoretically no minimum prey size exists, but the encounter rate, and therefore maximum clearance, is proportional to the linear size of the prey (Fenchel 1984; Monger and Landry 1990; cf. Fig. 1b).

However, size selectivity as expressed by the actual maximum clearance vs. prey size will deviate from the idealized spectra in Fig. 1a,b toward a more bell-shaped distribution. This deviation is due to variabilities in mesh size, prey size and shape, and the existence of boundary layers and electrostatic forces. Because of a lack of similarities, we have not attempted to fit the various observed size selectivity spectra to theoretical models. Instead, data were harmonized by the following procedure (cf. Fig. 1c). Data points of maximum clearance vs. prey size (or an equivalent measure of selectivity) were plotted on linear scales and connected by linear interpolation. The optimum prey size was defined as the data point showing maximum clearance. Prey size ranges corresponding to >50% and >10% of maximum clearance were determined to describe the width and skewness of the selectivity spectrum (Fig. 1c). Predator and prey sizes were expressed as equivalent spherical diameters [ESD = $(\text{vol.}/0.523)^{0.33}$].

Many studies express predator size in terms of body length or weight. We converted body length into body dry weight using regressions either from the actual study or from McCauley (1984). Dry weight was converted to carbon by a factor of 0.45 and carbon to volume by a factor of 8.3 $\mu m^3$ pg $C^{-1}$ (corresponding to 0.12 pg C $\mu m^{-3}$, e.g. Boraas 1983; Verity and Langdon 1984). In some studies where only body length was given and no applicable length-weight regression was found (e.g. Rothhaupt 1990), body volume was estimated by general geometrical formulae from McCauley (1984).

Information on size selectivity was extracted from studies covering representatives from various taxonomic groups of planktonic predators (Table 1). A plot of optimum prey size

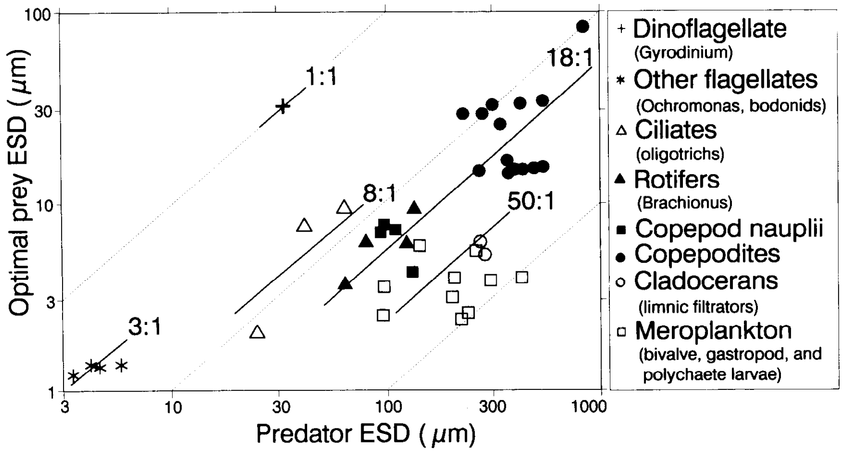

Fig. 2. Optimum prey size vs. predator size, both expressed as equivalent spherical diameter (ESD), data from Table 1. Lines represent average predator: prey size ratios for different groups of organisms (cf. Table 2).

against predator size (Fig. 2) shows predator: prey size ratios ranging from 1 : 1 to ~100 : 1 and thus fails to support the assumption of a general and fixed ratio. A significant scaling is, however, apparent within each taxonomic group, with a 1 : 1 ratio for the only heterotrophic dinoflagellate reported, 3 : 1 for other flagellates, 8 : 1 for the oligotrich ciliates, and 18 : 1 for the rotifers and meroplankton larvae. This scaling of the predator : prey size ratio is most evident for copepods, which also represent a major part of the data set, and least evident for meroplankton larvae, where optimum prey size seems to be uncorrelated with predator size. In an attempt to provide a tentative synthesis of the information given in Table 1, data for each taxonomic group were summarized by averaging predator : prey ratios (Table 2) and visualized as selectivity spectra (Fig. 3).

In view of the limited data base, these spectra must be considered provisional and not necessarily representative for the taxonomic groups. In order to evaluate whether the studied species represent the individual groups, we took qualitative data regarding the feeding mechanisms and type of prey into consideration.

Particle uptake is well documented in several planktonic flagellate groups (Patterson and Larsen 1991). The heterokonts (chrysophytes, bicoecids, pedinellids) and the kinetoplasts comprise a group of raptorial flagellates with observed predatory : prey size ratios from 2 : 1 to 8 : 1 (Fenchel 1982; Goldman and Caron 1985; Anderson et al. 1986; Chrzanowski and Šimek 1990; Moestrup and Andersen 1991). The prymnesiophytes have a different mechanism of prey capture but show similar size ratios (2 : 1 to 16 : 1; Green 1991; Kawachi et al. 1991).

The dinoflagellates, however, differ considerably from the other raptorial flagellates found in the plankton. The reported size ratios between prey and predator is within the range showed in Fig. 3 (0.4 : 1 to 7 : 1; e.g. Gaines and Elbrächter 1987; Jacobson and Anderson 1986; Strom 1991; P. J. Hansen 1991, 1992).

The choanoflagellates are filter feeders. The dimensions of their filter allow them to feed

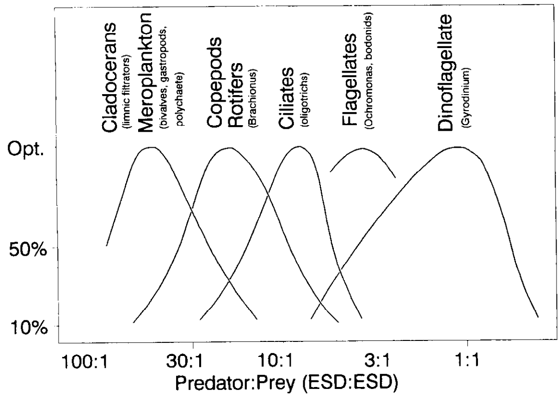

Fig. 3. Provisional size selectivity spectra for different pelagic predators based on information in Tables 1 and 2.

Table 1. Data from the literature on size selectivity by planktonic predators. Definitions of optimum, 50%-min, 50%-max, 10%-min, and 10%-max and calculation of predator ESD (equivalent spherical diameters) are given in Fig. 1 and text. All data in $\mu$m.

| Predator | ESD | Length | Opt. | 50%-min | 50%-max | 10%-min | 10%-max | Reference |
|---|---|---|---|---|---|---|---|---|
| Flagellates | | | | | | | | |
| *Ochromonas danica* | 6.1 | | 1.4 | | | | | Chrzanowski and Šimek 1990 |
| Bodo-like | 4.9 | | 1.4 | | | | | Chrzanowski and Šimek 1990 |
| Bodo-like | 4.4 | | 1.4 | | | | | Chrzanowski and Šimek 1990 |
| Bodo-like | 3.4 | | 1.3 | | | | | Chrzanowski and Šimek 1990 |
| *Gyrodinium spirale* | 28 | | 32 | 7.6 | 64 | 4.2 | 90 | P. J. Hansen 1992 |
| Ciliates | | | | | | | | |
| *Lohmaniella spiralis* | 66 | | 9.7 | 5.4 | 15.2 | 2.3 | 17.0 | Jonsson 1986 |
| *Strombidium reticulatum* | 42 | | 7.9 | 3.3 | 8.6 | 1.3 | 9.3 | Jonsson 1986 |
| *Strombidium vestitum* | 26 | | 2.1 | 1.6 | 2.9 | | 7.9 | Jonsson 1986 |
| Rotifers | | | | | | | | |
| *Brachionus angularis* | 66 | 120 | 3.5 | 1.0 | 5.7 | | 18.1 | Rothhaupt 1990 |
| *Brachionus* "strain F" | 83 | 150 | 6.1 | 2.7 | 12.6 | | 17.4 | Rothhaupt 1990 |
| *Brachionus* "strain B" | 126 | 230 | 6.0 | 2.1 | 16.7 | | | Rothhaupt 1990 |
| *Brachionus calyciflorus* | 139 | 250 | 8.8 | 6.2 | | 2.0 | | Rothhaupt 1990 |
| Meroplankton | | | | | | | | |
| *Mediomastus fragile* | 148 | 170 | 6.9 | 6.4 | 9.2 | 3.8 | 11.4 | B. Hansen 1993 |
| *Philine aperta* | 214 | 149 | 4.6 | 3.1 | 6.3 | | | B. Hansen 1991 |
| *P. aperta* | 280 | 239 | 6.5 | 4.0 | 16.7 | 1.5 | | B. Hansen 1991 |
| *P. aperta* | 317 | 274 | 4.4 | 3.9 | 6.6 | 1.5 | | B. Hansen 1991 |
| *P. aperta* | 441 | 392 | 4.5 | 3.9 | 7.4 | 1.8 | | B. Hansen 1991 |
| *Mercenaria mercenaria* | 100 | 136 | 4.1 | 3.5 | 5.2 | | 6.2 | Riisgård 1988 |
| *Mytilus edulis* | 99 | 120 | 2.9 | 1.4 | 5.4 | | 7.4 | Riisgård et al. 1980 |
| *M. edulis* | 236 | 175 | 2.9 | 2.1 | 4.5 | 1.8 | | Riisgård et al. 1980 |
| *M. edulis* | 241 | 175 | 2.9 | 2.5 | 6.9 | | | Riisgård et al. 1980 |
| *Ostrea edulis* | 208 | | 3.6 | | 8.4 | | | Walne 1965 |
| Copepod nauplii | | | | | | | | |
| *Acartia tonsa* N2-N3 | 97 | 140 | 6.8 | 5.4 | 7.9 | 4.9 | 11.1 | Berggreen et al. 1988 |
| *A. tonsa* N2-N3 | 100 | 145 | 7.2 | 6.1 | 14.7 | 4.5 | | Berggreen et al. 1988 |
| *A. tonsa* N2-N3 | 112 | 160 | 7.0 | 4.5 | 12.4 | 4.0 | | Berggreen et al. 1988 |
| *A. tonsa* N4-N5 | 135 | 190 | 4.0 | 3.6 | 17.5 | 2.6 | | Berggreen et al. 1988 |
| *Calanus pacificus* N5 | 237 | | 28.7 | 19.0 | 29.6 | 5.0 | | Fernandez 1979 |
| Copepodites | | | | | | | | |
| *Diaptomus sicilis* | 398 | | 14.1 | 8.9 | 22.0 | 4.0 | | Vanderploeg et al. 1984 |
| *A. tonsa* C3-C4 | 279 | 400 | 14.5 | 8.8 | | 4.4 | | Berggreen et al. 1988 |
| *C. pacificus* C1 | 289 | | 28.7 | 12.3 | | 7.0 | | Fernandez 1979 |
| *A. tonsa* males | 453 | 700 | 14.5 | 11.2 | 91.0 | 4.0 | 153.0 | Berggreen et al. 1988 |
| *A. tonsa* females | 499 | 1,000 | 14.8 | 11.1 | 77.0 | 4.4 | 137.0 | Berggreen et al. 1988 |
| *Pseudocalanus minutus* | 414 | | 14.4 | 6.0 | 28.0 | 4.5 | 32.0 | Poulet 1977 |
| *Temora longicornis* | 558 | | 15.0 | 6.5 | 33.0 | | | Poulet 1977 |
| *Acartia clausi* | 353 | | 25.0 | | 35.0 | | | Poulet 1977 |
| *Eurytemora herdmani* | 381 | | 16.0 | 8.0 | 33.0 | 6.7 | | Poulet 1977 |
| *Calanus finmarchicus* | 855 | | 80.0 | 27.0 | 137.0 | 7.0 | | Kiørboe and Runge unpubl. |
| *A. tonsa* | 444 | | 32.0 | | | | | Wilson 1972 |
| *Diaptomus graciloides* | 325 | | 31.0 | 27.0 | 35.0 | | | Gliwicz 1977 |
| *Centropages typicus* | 559 | | 32.0 | 25.0 | 37.0 | 9.2 | 120.0 | Wolgemuth unpubl. |
| Cladocerans | | | | | | | | |
| *Daphnia cuculata* | 284 | | 7.0 | | 15.0 | | 24.0 | Gliwicz 1977 |
| *Daphnia longispina* | 297 | | 6.0 | | 20.0 | | 25.0 | Gliwicz 1977 |
| *Bosmina coregoni* | 311 | | | | 12.0 | | 24.0 | Gliwicz 1977 |
| *Chydorus sphaericus* | 344 | | | | 11.0 | | 20.0 | Gliwicz 1977 |
| *Diaphanosoma brachyurum* | 277 | | | | 10.0 | | 17.0 | Gliwicz 1977 |

Table 2. Summary of literature data on size selectivity by planktonic predators, based on Table 1 (terms defined in Fig. 1 and text). All data expressed as ratios between predator and prey equivalent spherical diameters (ESD). Averages ± standard errors (calculated on log-transformed data) and number of observations (in parentheses) are given.

| Predator | Predator : prey size (ESD : ESD)<br>Opt. | 50%-min | 50%-max | 10%-min | 10%-max |
|---|---|---|---|---|---|
| Ciliates | 8±2 (3) | 13±1 (3) | 6±1 (3) | 31±1 (3) | 4±1 (3) |
| Rotifers | 17±2 (4) | 42±11 (4) | 8±1 (3) | 69 (1) | 4±1 (2) |
| Meroplankton | 50±9 (10) | 66±13 (9) | 9±5 (10) | 138±48 (5) | 14±1 (3) |
| Nauplii | 18±4 (4) | 23±4 (4) | 9±1 (4) | 28±6 (4) | 9 (1) |
| Copepodites | 18±3 (14) | 33±6 (12) | 10±1 (11) | 76±9 (10) | 5±2 (4) |
| Cladocerans | 45±3 (2) |  | 23±3 (5) |  | 14±1 (5) |

on the smallest bacteria, suggesting a predator : prey ratio up to 30 : 1 (Andersen 1988/1989). However, large prey apparently can also be ingested (predator : prey ratios from 2 : 1 to 7 : 1; Fenchel 1982; Geider and Leadbetter 1988; Andersen 1988/1989).

Observations on the spirotrich ciliates (oligotrichs and tintinnids) confirm the range shown in Fig. 3 (2.5 : 1 to 30 : 1; Heinbokel 1978; Spittler 1973; Rassoulzadegan 1978, 1982; Rassoulzadegan and Etienne 1981). Prostomatids (e.g. *Tiarina, Balanion, Holophrya*) and Litostomatids (e.g. *Didinium*) have very flexible cytostomes, allowing them to ingest prey of their own size. The observed size ratio between predator and prey range from 1 : 1 to 30 : 1 (Klaveness 1984; Stoecker et al. 1986; Madoni et al. 1990). Some (e.g. *Coleps*) are even histophagous (feeding on large wounded prey, Klaveness 1984). Scuticociliates show size ratios from 10 : 1 to 30 : 1 (Fenchel 1980).

Most planktonic rotifers are filter feeders with predator : prey size ratios as described in Fig. 3 (5 : 1 to 32 : 1; e.g. Pilarska 1977; Pourriot 1977; Hino and Hirano 1980; Starkweather et al. 1979). Some rotifers are, however, raptorial feeders (e.g. the order Ploima, the genus *Asplanchna*), with size ratios of 1.5 : 1 to 5 : 1 (Pourriot 1977; Gilbert 1978, 1985; Gilbert and Stemberger 1985; Gilbert and Kirk 1988). The genus *Synchaeta* is both filtrator and raptorial with size ratios of 1.5 : 1 to 17 : 1 (Egloff 1988).

Observations on meroplankton larvae with double cilia bands (Annelida, Echiorida, Mollusca, Nemertini, and Entoprocta) follow the pattern shown in Fig. 3, with predator : prey size ratios of 30 : 1 to 125 : 1 (Daro and Polk 1973; Chia and Koss 1978; Sprung 1984, 1989). For meroplankton with a single cilia band (Phoronidae, Brachiopoda, Echinodermata, and Enteropneusta), wide retention spectra are reported (Strathmann 1971; Rassoulzadegan and Fenaux 1979; Rassoulzadegan et al. 1984). These larvae are observed to ingest relatively large particles, with predator : prey size ratios down to ~5 : 1 for the largest particles ingested (Strathmann 1971; McEdward 1984).

Most planktonic copepods are suspension feeders. Many genera are described as more or less mechanical filter feeders (e.g. *Temora, Pseudocalanus, Paracalanus,* and *Diaptomus*; Vanderploeg 1981; Tiselius and Jonsson 1991). Several genera are both filtrators and raptorial feeders (e.g. *Calanus, Acartia, Centropages, Eucalanus, Diaptomus, Aetidius, Oithona,* and *Cyclops*) depending on the prey size (Robertson and Frost 1977; Richman et al. 1980; Lampitt and Gamble 1982; Strickler 1984; Price and Paffenhöfer 1986; Vanderploeg et al. 1988; Tiselius 1989; Jonsson and Tiselius 1990). Field studies reveal that they exploit prey sizes over a wider range than presented in Fig. 3, especially in terms of the minimum particle size; they have a predator : prey size ratio of 3 : 1 to 180 : 1 (e.g. Poulet 1973, 1977; O'Conners 1980) but an optimal particle size ratio down to 65 : 1 (e.g. Paffenhöfer and Knowles 1978; Vanderploeg 1981; Vanderploeg and Paffenhöfer 1985).

Some pelagic copepods are, however, strictly raptorial (some species of the genera *Cyclops,* and calanoid genera like *Euchaeta, Pareuchaeta, Labidocera, Tortanus,* and *Anomalocera*; Anraku and Omori 1963; Whitehouse and Lewis 1973; Brandl and Fernando 1978; Kerfoot 1978). The raptorial species often have the ability to macerate their prey. The size ratio between predator and prey is, however, often not correlated to predictable structural limitations but rather is a handling problem (Vanderploeg et al. 1988).

Among the planktonic cladocerans, two fundamentally different feeding modes are developed. For raptorials (Onychopoda: *Evadne, Podon, Bothotrephes,* and *Polyphemes*; and Haplopoda: *Leptodora*), for which the upper size limit is large to infinite because of grasping, the size ratio between predator and prey is reported to be 1 : 1 to 17 : 1 (Nival and Ravera 1979; Nielsen 1991). All other cladocerans (Anomopoda) are filter feeders, and more or less mechanical filtering is described for some genera (*Daphnia, Diaphanosoma, Chydorus, Bosmina*) (Gliwicz 1969; Hessen 1985). A continuum for mechanical filter feeding to raptorial feeding is suggested, with a certain discriminative feeding mode for *Bosmina* (DeMott 1982; Bern 1990) and a specialization on larger particles for *Holopedium* (Hessen 1985). The predator : prey ratio ranges from 5 : 1 to 18 : 1 for the maximum and optimum particle sizes, but for the minimum particle sizes a predator : prey ratio up to 1 : 1,000 is reported (e.g. Burns 1968; McMahon and Rigler 1965; DeMott 1982; Hessen et al. 1986; Vaqué and Pace 1992).

In general, the qualitative information from the literature supports the pattern that emerges from the limited number of quantitative studies (Fig. 3); however, exceptions do occur in almost all groups, as described above. In particular, a difference between filter feeders and raptorial-intercept feeders is seen across taxonomic groups.

Quantitative information on size selectivity by planktonic predators is scarce, especially for raptorials and microphagous filtrators (e.g. cladocerans), i.e. for those predators that deviate furthest from the often assume 10 : 1 predator : prey size ratio. When more solid information on the size selectivity of these organisms becomes available, it may be possible to categorize heterotrophic plankton into functional groups based on feeding mechanisms rather than taxonomy.

Food-web structure is a flexible attribute of pelagic ecosystems. The actual dominance of predators with preference for smaller or larger prey will influence the number of steps in the food chains (i.e. the number of trophic levels sensu Lindemann 1942) and thereby determine whether primary production is efficiently passed to larger organisms or remineralized (the "link-or-sink" question; Williams 1981; Sherr and Sherr 1988).

The complex pattern that emerges from Figs. 2 and 3 suggests difficulty in constructing a simple size-based model of the pelagic food web (Longhurst 1990). The different functional groups, however, rarely occur simultaneously in the same location. Thus, the freshwater mesozooplankton is usually dominated by either copepods or cladocerans and coastal microzooplankton by either ciliates or dinoflagellates. With more knowledge about the size selectivity of the various functional groups of the zooplankton and about their actual occurrence in a given pelagic environment, it should be possible to construct a reliable yet simple size-based model of the pelagic food web for that particular situation.

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*Submitted: 5 August 1992*
*Accepted: 16 December 1992*
*Amended: 29 April 1993*