

A review of planktivorous fishes: Their evolution, feeding behaviours, selectivities, and impacts

Xavier Lazzaro

ORSTOM (*Institut Français de Recherche Scientifique pour le Développement en Coopération*), 213, rue La Fayette, 75480 Paris Cedex 10, France

Present address: *Laboratorio de Limnología, Centro de Recursos Hídricos e Ecología Aplicada, Departamento de Hidráulica e Saneamiento, Universidad de São Paulo, Av. Dr. Carlos Botelho, 1465, São Carlos, SP. 13560, Brazil*

Mail address: C.P. 337, São Carlos, SP. 13560, Brazil

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Résumé

La vision classique des limnologistes fut de considérer les interactions entre les composants des écosystèmes lacustres comme un flux d'influence unidirectionnel des sels nutritifs vers le phytoplancton, le zooplancton, et finalement les poissons, par l'intermédiaire de processus de contrôle successivement physiques, chimiques, puis biologiques (Straškraba, 1967). L'effet exercé par les poissons planctophages sur les communautés zoo- et phytoplanctoniques ne fut reconnu qu'à partir des travaux de Hrbáček *et al.* (1961), Hrbáček (1962), Brooks & Dodson (1965), et Straškraba (1965). Ces auteurs montrèrent (1) que dans les étangs et lacs en présence de poissons planctophages prédateurs visuels, les communautés zooplanctoniques étaient composées d'espèces de plus petites tailles que celles présentes dans les milieux dépourvus de planctophages et, (2) que les communautés zooplanctoniques résultantes, composées d'espèces de petites tailles, influençaient les communautés phytoplanctoniques. Bien que la variabilité de la réponse du phytoplancton à la prédation par les poissons révèle l'importance d'autres facteurs (tels que la limitation en sels nutritifs et la compétition interspécifique des algues), ces travaux démontrent que les communautés zoo- et phytoplanctoniques pouvaient effectivement être affectées par l'alimentation sélective des poissons planctophages. Pendant les deux dernières décennies, de nombreux travaux en limnologie se sont concentrés sur cet impact radical des poissons sur les communautés planctoniques. La réponse directe des communautés zooplanctoniques à la prédation visuelle des poissons planctophages (appelés en anglais ‘particulate feeders’) a suscité un intérêt tout particulier, alors que les effets multiniveaux causés par les poissons planctophages filtreurs (prédation sur le zooplancton plus broutage du phytoplancton) ont été plus rarement abordés. Les objectifs de cette révision sont de documenter les inter-relations poissons-plancton, afin (1) d'obtenir des éléments d'appréciation de l'impact des poissons sur les communautés planctoniques, et (2) d'établir des modèles mécanistiques d'alimentation planctophage tenant compte du répertoire alimentaire et de la sélectivité du poisson, des réponses adaptatives du plancton, et des conditions du milieu.

L'approche utilisée ici est basée sur des résultats expérimentaux de terrain et de laboratoire provenant de la littérature concernant les systèmes tropicaux et tempérés d'eau douce (parfois marine). Quatre groupes de poissons planctophages sont distingués: les prédateurs visuels limités par la taille de leur bouche (c'est-à-dire les larves et les espèces de petites tailles: ‘gape-limited predators’), les prédateurs visuels proprement dit (‘particulate feeders’), les filtreurs par pompage (‘pump filter feeders’), et les filtreurs par déplacement (‘tow-net

filter feeders'). Pour chaque groupe, les mécanismes de sélection des proies sont analysés, aussi bien du point de vue du prédateur que de la proie. Afin de rechercher les mécanismes déterminant la sélectivité alimentaire du prédateur et de discuter ses effets potentiels sur les communautés de proies, l'acte de prédation est décomposé en une séquence d'événements successifs (Holling, 1966): la détection, la poursuite, la capture, la rétention et la digestion pour les prédateurs visuels; et la capture, la rétention et la digestion pour les filtreurs. Les avantages et les inconvénients de plusieurs mesures de sélectivité (appelées indices d'électivité), aussi bien que leur utilisation appropriée sont discutés. Les modèles de sélection de proies et les théories de recherche optimale sont analysés pour les différents modes d'alimentation des planctophages. Des modèles mécanistiques basés sur l'approche de Holling (loc. cit.) sont proposés pour chaque mode d'alimentation afin de déterminer les vulnérabilités différencielles des proies et l'amplitude optimale de la diète.

Cette révision concerne les domaines de l'écologie générale, de la limnologie, de l'aménagement des pêcheries (tel que, par exemple, l'utilisation des ressources planctoniques, le repeuplement, l'introduction, ou le maintien de populations naturelles de poissons), et du contrôle biologique des processus d'eutrophisation (approches par biomanipulation). Elle insiste sur le réel besoin de connaissances sur la sélectivité alimentaire et l'utilisation de la nourriture par les poissons planctophages. Elle permet de conclure que prédateurs et proies sont intimement et mutuellement adaptés. Aussi, dans la plupart des cas, il apparaît peu approprié d'aborder la dynamique du plancton et la qualité des eaux sans tenir compte de l'estimation des pressions de prédation et de broutage exercées par les poissons planctophages.

Abstract

The classical approach of limnologists has been to consider the interactions between lake ecosystem components as an unidirectional flow of influence from nutrients to the phytoplankton, to the zooplankton, and finally to the fish, through successive controls by physical, chemical, and biological processes (Straškraba, 1967). The effect of planktivorous fishes on zooplankton and phytoplankton communities was not recognized until the studies of Hrbáček *et al.* (1961), Hrbáček (1962), Brooks & Dodson (1965) and Straškraba (1965). They showed that (1) in ponds and lakes in the presence of planktivorous fishes the zooplankton communities were composed of smaller bodied species than in those lacking planktivores, and (2) the resulting small-bodied zooplankton communities affected the phytoplankton communities. Although the variability of the phytoplankton response to fish predation showed the importance of other factors (such as nutrient limitation and interspecific competition of algae), these studies emphasized that zooplankton and phytoplankton communities can be affected by the feeding selectivity of planktivorous fishes. During the last two decades, many limnological studies have focused on this dramatic impact of fish on plankton communities. The direct response of zooplankton communities to visual fish predation (i.e. particulate feeding) has been of major interest, whereas the multilevel effects of filter-feeding fish (predation on zooplankton plus grazing on phytoplankton) have been neglected. The objectives of this review are to document fish-plankton interrelationships in order to (1) provide insights into the impact of fish on plankton communities, and (2) outline mechanistic models of planktivory according to the feeding repertory and the selectivity of the fish, the adaptive responses of the plankton, and the environmental conditions.

The approach adopted here is based on field and laboratory experimental results derived from the literature on tropical and temperate freshwater (occasionally marine) systems. Four types of planktivorous fish are distinguished: the gape-limited larvae and small fish species, the particulate feeders, the pump filter feeders, and the tow-net filter feeders. For each type of planktivore, the mechanisms of prey selection are analyzed from the point of view of both the predator and the prey. To investigate the main determinants of the predator feeding selectivity, and to discuss its potential effects on prey communities, the predation-act is divided into a sequence of successive events (Holling, 1966): detection, pursuit, capture, retention, and digestion for particulate feeders; and capture, retention, and digestion for filter feeders. The strengths and weaknesses of various measures of selectivity (i.e. electivity indices), as well as their appropriate usages are considered. Available prey selection models and optimal foraging theories are analyzed for the different planktivore feeding

modes. Mechanistic models based on Holling's (*loc. cit.*) approach are proposed for each feeding mode to determine differential prey vulnerabilities and optimal diet breadth.

This review has application to several fields, including general ecology, limnology, fisheries management (for example, utilization of planktonic resources, stocking, introduction, or maintenance of natural fish populations), and biological control of the eutrophication processes (biomanipulation approaches). It emphasizes the real need for more knowledge of the feeding selectivity and food utilization of planktivores. It concludes that predator and prey are mutually adapted. Thus, in most cases, study of plankton dynamics and water quality should include the assessment of fish predation and grazing pressures.

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I. Evolution of plankton-feeding fishes

A. From macrophages towards microphages

The oldest teleostean fishes evolved as generalized predators (Gosline, 1971) feeding on comparatively large prey (macrophagy). The main divergence from this basic pattern is a trend towards feeding on smaller prey (microphagy), such as the plankton. This evolution from macrophagy to microphagy is marked by the development of specialized structures and the regression of others, such as: modification of jaws from fixed to protrusible, replacement of teeth by elaborate gill rakers on the branchial arches, modification of some gill rakers in an epibranchial organ on the roof of the mouth, lengthening of the digestive tract (Harder, 1960; Marshall, 1965; Nelson, 1967, 1970; Durbin & Durbin, 1975) to process larger amounts of fine material without necessity of a digestive pause between meals (which is the rule in macrophages).

Members of the order Clupeiformes, the herring-like fishes, illustrate well this trend towards microphagy: for example, the progression from the tarpon-like ancestor (a predatory macrophage) to the round-herring (a particulate-feeding microphage) to the alewife (a particulate and filter-feeding microphage) to the menhaden (a filter-feeding microphage) (Durbin, 1979).

The most specialized of the microphages are the filter-feeding species. The menhaden, a filter-feeding clupeid microphage, repeats most of these evolutionary steps during the life of a single fish. The selective predation of larval menhaden is directed towards individual zooplankton: mainly copepods (June & Carlson, 1971). During the metamorphosis, particulate feeding is gradually replaced by filter feeding on zooplankton, phytoplankton, and fine detritus (Durbin & Durbin, 1975).

Only a small fraction of the energy produced by the phytoplankton can be transferred through the food chain to the higher trophic levels, usually predatory macrophages. On the contrary, a greater fraction is available for plankton-feeding fishes. This is reflected in the abundance of planktivorous fishes in freshwater rivers and lakes (for example, Jenkins (1967) showed that omnivorous *Dorosoma cepedianum* and *D. petenense* account for 40% of fish standing crops in central U.S. reservoirs), in areas of coastal marine upwellings (Ryther, 1969),

and in the open sea. Planktivores are involved in the main commercial fisheries of the world (anchovies, sardines, herrings, menhaden, salmonids, and many others), and in recreational fisheries (sunfish, trout, salmon, mackerel, etc.). Today, teleosts include more than 95% of the living species of fish (Marshall, 1965), and microphagy is advanced in most of the (freshwater, at least) orders:

- even in Acipensiformes (not teleostean but actinopterygian):
 - Polyodontidae: paddlefish, *Polyodon spathula* (Rosen & Hales, 1981);
- especially in Clupeiformes:
 - Clupeidae (Hildebrand, 1963; Longhurst, 1971; Blaber, 1979): West African shads, *Ethmalosa fimbriata* (Fagade & Olanayan, 1972), and *E. dorsalis* (Bainbridge, 1957, 1963); gizzard shad, *Dorosoma cepedianum* (Velasquez, 1939; Kutkuhn, 1957; Smith, 1963; Drenner, 1977; Drenner *et al.*, 1978, 1982a, 1982b, 1984a; Barger & Kilambi, 1980; Drenner & McComas, 1980); threadfin shad, *D. petenense* (Holanov & Tash, 1978); alewife, *Alosa pseudoharengus* (Brooks & Dodson, 1965; Wells, 1970; Hutchinson, 1971; Rhodes, 1971; Warshaw, 1972; Rasmussen, 1973; Rhodes & McComish, 1975; Gannon, 1976; Janssen, 1976, 1978a, 1978b, 1980); blueback herring, *Alosa aestivalis* (Brooks & Dodson, 1965; Hutchinson, 1971; Janssen, 1982); Pacific sardine, *Sardinops sagax* (Lewis, 1929; Arthur, 1976; Nelson, 1979); Tanganyika sardine, *Limnothrissa miodon* (Begg, 1976); Indian oil sardine, *Sardinella longiceps* (Bensam, 1964); thread herrings, *Opisthonema* spp. (Berry & Barret, 1963); North Atlantic and North Pacific herring, *Clupea harengus* (Blaxter & Holliday, 1963; Blaxter, 1966; Rosenthal, 1969; Rosenthal & Hempel, 1970); Atlantic menhaden, *Brevoortia tyrannus* (June & Carlson, 1971; Peters, 1972; Durbin & Durbin, 1975; Jeffries, 1975); pilchard, *Sardinops ocellata* (King & McLeod, 1976);
 - Engraulidae: Northern anchovy, *Engraulis mordax* (Leong & O'Connell, 1969; Loukashkin, 1970; O'Connell, 1972; Arthur, 1976; Nelson, 1979); Southwest African anchovy, *E. capensis* (King & McLeod, 1976); Peruvian anchoveta, *E. ringen* (Rojas de Mendiola,

- 1971); anchoveta, *Cetengraulis mysticetus* (Bayliff, 1963); *Stolephorus* spp. (Blaber, 1979);
- in Salmoniformes:
 - Salmonidae: whitefishes and ciscoes, *Coregonus* spp. (Bertmar & Stromberg, 1969; Kliewer, 1970; Rasmussen, 1973; Giussani, 1974; Seghers, 1975; Engel, 1976; Janssen, 1978a, 1980) and *Leucichthys* spp. (Clemens & Bigelow, 1922); Pacific salmon, *Oncorhynchus nerka* (Narver, 1970; Feller & Kaczynski, 1975; Engel, 1976; Eggers, 1978, 1982); trout, char (Nilsson, 1960, 1963), and Atlantic salmon, such as rainbow trout, *Salmo gairdneri* (Hartman, 1958; Galbraith, 1967; Ware, 1971, 1972, 1973); cutthroat trout, *S. clarki* (Andrusak & Northcote, 1971; Schutz & Northcote, 1972; Northcote *et al.*, 1978); lake trout, *Salvelinus namaycush* (Kettle & O'Brien, 1978) and Dolly Varden, *S. malma* (Andrusak & Northcote, 1971; Schutz & Northcote, 1972; Northcote *et al.*, 1978); brook charr, *Salvelinus fontinalis* (Dawidowicz & Gliwicz, 1983);
 - Osmeridae: smelt, *Osmerus mordax* (Reif & Tappa, 1966; Rasmussen, 1973);
 - in Myctophiformes:
 - Myctophidae: 'lantern fishes' (Nafpaktitis *et al.*, 1977);
 - in Cypriniformes:
 - Characidae: *Alestes baremoze* (Green, 1967; Lauzanne, 1970, 1973, 1977); *Hydrocyrus forskalii* (Lauzanne, 1977);
 - Gymnotidae: *Rhabdolichops troscheli* (Maggio-Leccia & Zaret, 1978);
 - Cyprinidae: goldfish, *Carassius auratus* (Hester, 1968); carp, *Cyprinus carpio* (Hrbáček *et al.*, 1961, 1978; Grygierek, 1962; Hrbáček, 1962, 1969; Hillbricht-Ilkowska, 1964; Grygierek *et al.*, 1966; Prejs, 1973; Losos & Hetesa, 1973; Kajak *et al.*, 1976); silver carp, *Hypophthalmichthys molitrix* (Savina, 1965; Borutskij, 1973; Omarov & Lazareva, 1974; Vovk, 1974; Januszko, 1974; Kajak *et al.*, 1975, 1977; Kajak, 1977; Opuszynski, 1979a, 1979b, 1980); bream, *Aramis brama* (Lammens, 1985), and tench, *Tinca tinca* (although both species are opportunistic and more generally benthophagous; Prejs, 1973; Hillbricht-Ilkowska *et al.*, 1973;
 - Hillbricht-Ilkowska & Weglenska, 1973); bleak, *Alburnus alburnus* L. (Prejs, 1976); crucian carp, *Carassius carassius* L. (Prejs, 1973);
 - Castotomidae: bigmouth buffalo, *Ictiobus cyprinellus* (Staroska & Applegate, 1970);
 - in Siluriformes:
 - in Cyprinodontiformes:
 - in Atheriniformes:
 - in Gasterosteiformes:
 - in Perciformes:
 - Gasterosteidae: three-spined stickleback, *Gasterosteus aculeatus* (Beukema, 1968; Gibson, 1980); fifteen-spined stickleback, *Spinachia spinachia* (Kislalioglu & Gibson, 1976);
 - Mugilidae: mullets, genus *Mugil* (Norman & Greenwood, 1963; Thomson, 1966);
 - Helostomidae: *Helostoma temmincki* (Liem, 1967);
 - Centrarchidae: bluegill sunfish, *Lepomis macrochirus* (Werner, 1972, 1974, 1977; Werner & Hall, 1974, 1976, 1977, 1979; Vinyard & O'Brien, 1975, 1976; O'Brien *et al.*, 1976; Werner *et al.*, 1977, 1981, 1983a, 1983b; Vinyard, 1980; Gardner, 1981; Mittelbach, 1981; Janssen, 1982); northern longear sunfish, *Lepomis megalotis peltastes*, and pumpkinseed, *L. gibbosus* (Laughlin & Werner, 1980); white crappie, *Pomoxis annularis* (Wright *et al.*, 1983; Wright & O'Brien, 1984); largemouth bass fry, *Micropterus salmoides* (Elliot, 1976);
 - Percidae: Eurasian perch, *Perca fluviatilis* (Guma'a, 1978; Furnass, 1979; Stenson, 1980); yellow perch, *P. flavescens* (Galbraith, 1967; Wong & Ward, 1972; Rasmussen, 1973);
 - Cichlidae: Congo tilapia, *Tilapia rendalli* (Caulton, 1976); blue tilapia, *T. aurea* (Spanaru & Zorn, 1978; Gophen *et al.*, 1983a,

1983b; Drenner *et al.*, 1984b); *T. esculenta* (Greenwood, 1953); *T. nilotica* (Moriarty, 1973; Moriarty & Moriarty, 1973); *Sarotherodon galilaeus* (Lauzanne & Iltis, 1975; Spataru, 1976; Spataru & Zorn, 1976; Lauzanne, 1977; Gophen, 1980; Drenner *et al.*, 1982c; Gophen *et al.*, 1983a, 1983b); *Haplochromis nigripinnis* (Moriarty & Moriarty, 1973); • Carangidae: jack mackerel, *Trachurus symmetricus* (Carliste, 1971; Arthur, 1976); • Scombridae: *Pneumatophorus* spp. (Godsil, 1954); Indian mackerel, *Rastrelliger kanagurta* (Bhimachar *et al.*, 1960; Jones & Rosa, 1965; Colin, 1976; Nelson, 1979); Pacific mackerel, *Scomber japonicus* (O'Connell & Zweifel, 1972); wavyback skipjack, *Euthynnus affinis* (Walters, 1966).

This list is not exhaustive. More general information on trophic relationships between various planktivorous fish species is available in Bigelow & Schroeder, 1953; Berg & Grimaldi, 1966; Keast & Webb, 1966; Nelson, 1967; Grimaldi, 1972; Roberts, 1972; Fryer & Iles, 1972; Davis & Birdson, 1973; Prejs, 1973, 1976; Nilsson & Pejler, 1973; Giussani, 1974; Hobson, 1974; Merret & Roe, 1974; Lowe-McConnell, 1975; De Bernardi & Giussani, 1975; Svardson, 1976; Lauzanne, 1977; Nelson, 1979; Zaret, 1980; Pourriot *et al.*, 1982, and Pourriot, 1983.

B. Evolution of mouth protrusibility

Jaw protrusibility is an advance in mouth evolution (Alexander, 1967a), and is found in numerous species of living teleosts (Marshall, 1965; Gosline, 1971), mainly among Acanthopterigians, Cyprinidae, and Cyprinodontidae (Atheriniformes). In a recent review paper, Motta (1984) described four basic mechanisms of jaw protusion and pointed out that: (1) the mandibule depression is the most common mechanism among the fish studied, (2) the twisting action of the maxilla has been overemphasized in the past, and (3) the neurocranial elevation and the suspensorial abduction may be more prevalent than realized. Of the 15 cited functions, some present an adaptative value for plankton capture, among them: (1) moving the mouth suddenly nearer the prey and so increasing the velocity of attack and reducing the volume of water that must be sucked in, (2) increasing the initial suction force of the water flow (because the diameter of the pro-

truded mouth is often smaller than that of the unprotruded mouth) particularly when associated with a round protruded mouth orifice (better adapted for sucking prey items than a 'grinning' or slit-shaped mouth), (3) increasing the distance from which the fish can remove prey items by 25 or 50% of the head length, (4) closing the mouth in the protruded position on a prey item so tending to hold it straight, pointed towards the gullet (i.e. preventing misdirection of the suction force and presumably facilitating swallowing), and increasing the volume of water sucked into the mouth without being blown out again as the mouth closes, (5) adapting the feeding movement to the position, behaviour and nature of the prey item by adjustable position mechanisms, and (6) serving to align the direction of the bite with that of the pushing developed by the caudal and pectoral fins during feeding. Motta (loc. cit.) emphasized that the protrusible jaws of cichlids are highly coordinated and versatile. It results in a continuous modulated jaw mechanism whose adaptive significance is the ability to make a wide variety of rapid adjustments in the gape, biting force, and degree of protrusion according to the changing position, behaviour and nature of the prey item (Liem, 1980a). The different feeding behaviours displayed may result in differential capture efficiencies (Liem, 1980b).

Protrusion may have a selective advantage, through competition, in fishes with food habits which overlap. As an example, differential mouth morphologies resulted in a replacement of the brook silverside (*Labidesthes sicculus*) by the inland silverside (*Menidia beryllina*) in Lake Texoma (Texas Oklahoma border). These two atherinids use similar habitats and feed selectively on the largest prey they can capture (McComas & Drenner, 1982). Since *Menidia* has a protrusible and tube-shaped mouth, it can capture evasive copepods more successfully than the v-notched mouth of *Labidesthes*.

II. Feeding modes

A. Obligate and facultative planktivores

Most fishes feed on plankton during at least some period of their lives. Planktonic fish larvae consume zooplankton and, sometimes, phytoplankton. Many species switch to larger prey

and leave planktivory as they grow, whereas others feed during their entire lives on plankton. Some are obligate planktivores feeding exclusively on plankton; others are facultative planktivores feeding on plankton as well as on other food items.

The majority of works concerning fish feeding on plankton have been dedicated to facultative planktivores (such as sunfishes, *Lepomis* spp.). Facultative planktivores are more generally restricted to littoral areas where food resources are more diverse. They are opportunistic feeders, switching to food sources other than plankton (like suspended organic particles, periphyton, macrophytes, aquatic or terrestrial insects, seeds, benthic or sub-benthic animals or plants) during some periods of the year when plankton is less available. For example, as emphasized by Lauzanne (1977), in Lake Chad during low water level conditions (dry season), *Brachysynodontis batensoda* (a nocturnal filter-feeding Mochocidae) switches from an exclusive zooplankton diet to a mixed zooplankton and swimming larval and nymphal insect diet, while *Alestes dentex* (Characidae) begins feeding on, besides zooplankton, insects (immature stages of Chironomids, Trichoptera, Ephemeroptera, and Hemiptera, but mostly swimming larvae of *Chao-borus*), and seeds (Graminea and Cyperaceae).

There have been less works on the feeding mechanics of obligate planktivores (such as alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*), probably because they are extremely delicate and difficult to capture alive (Janssen, 1982). Obligate planktivores, such as herrings, live only in pelagic areas where planktonic resources are dominant.

Comparing the searching behaviours for zooplankton in an obligate planktivore, blueback herring (*Alosa aestivalis*) and in a facultative planktivore, bluegill (*Lepomis macrochirus*), Janssen (loc. cit.) observed that the methods used by the two fishes are markedly different. Blueback herring uses a very effective search method for zooplankton as it searches while swimming, whereas bluegill searches while stopped (hovering), swimming to a prey only as soon as it is detected (see section III.A.1.).

B. Particulate feeders, pump and tow-net filter-feeders: definitions

Planktivorous fishes use two distinct behaviours

to feed on plankton: particulate feeding and filter feeding.

A) Particulate feeders attack single individual planktonic prey item which they visually select from the water column (Confer & Blades, 1975; Janssen, 1976, 1978a, 1980, 1981, 1982; Werner, 1977; Vinyard, 1980). Nevertheless, several prey may be inhaled incidentally during the capture of the pursued prey (Wright *et al.*, 1983).

In contrast, both pump filter feeders and tow-net filter feeders do not visually detect individual prey item, but engulf a volume of water containing the food organisms, and retain the planktonic prey and particles by passing this volume of water over entrapment structures, such as, principally, gill rakers, microbranchiospines on the gill arches, and branchial tooth plates.

B) Tow-net filter feeders surround the prey items with their mouths which are held fully agape while swimming rapidly (Walters, 1966; Durbin & Durbin, 1975; Colin, 1976; Rosen & Hales, 1981).

C) Pump filter feeders use rhythmic suctions to capture prey items, while swimming slowly, or remaining quite stationary (Moriarty *et al.*, 1973; Drenner, 1977; Janssen, 1976, 1978a, 1980; Holanov & Tash, 1978; Drenner & McComas, 1980; Drenner *et al.*, 1978, 1982a, 1982b, 1982c, 1984a; Gophen *et al.*, 1983b).

I will use the above terminology in this review, but other terminologies may be appropriate as well. Hillbricht-Illkowska (in litt.) emphasizes that, regardless to the terminology commonly employed, both particulate and filter feeders are feeding on 'particles'. Thus, they are rather 'particulate-seizing feeders' and 'particulate-filtering feeders', respectively. But, to avoid using the word 'particulate', 'visual feeders' may be matched with 'filter feeders'.

An intermediate feeding mode is described as ' gulping' by Janssen (1976, 1978a) for the alewife, *Alosa pseudoharengus*, and the cisco, *Coregonus artedii*. The fish use short sequences of several pumps which alternate with pauses of about 0.5 second. Although very similar to ' gulping', 'pump filter feeding', described by Drenner (1977) for gizzard shad, *Dorosoma cepedianum*, is not identical. The shad consecutively opens and closes its mouth, pumping in water at a maximum rate of 2–3 times per second, while swimming rather slowly. According to Janssen (in litt.), the major difference is that gulping is visual (at least in the light), and alewives

and ciscoes are size selective using this mode. Janssen (1981) could alter the direction of gulping of blueback herring, *Alosa aestivalis*, by altering the lighting scheme (i.e., the orientation of the 'Snell's window'). While not mentioned in the paper, Janssen (in litt.) could shift those fish towards tow-net filter feeding by turning off the light (dim red light on). Unless there is no change in prey density, turning the light back on induces gulping again. Moreover, ciscoes under similar circumstances continue to gulp, apparently not selectively. Gulping is not directed to one prey item, but it is visually oriented and size selective, and thus it must be classified as particulate feeding.

C: Switching from particulate to filter-feeding modes

Dependence on fish age. For some fishes, the feeding mode used to capture plankton is dependent on fish size (i.e., fish age). When adult, some are obligate filter feeders. For example, adult Atlantic menhaden, *Brevoortia tyrannus*, is an obligate filter feeder (Durbin & Durbin, 1975), but is a particulate feeder when larval and prejuvenile (smaller than 40 mm TL) (June & Carlson, 1971). An identical evolutionary pattern is observed during ontogeny in the cichlids, *Tilapia aurea* and *Sarotherodon galilaeus* (Gophen *et al.*, 1983a, 1983b), and others. Those fishes are obligate particulate feeders when larval and juvenile and mainly filter feeders when adult ('obligate' may not be appropriate as *T. aurea* feed as a scraper even when very large; Drenner, in litt.). A transition period exists during which both feeding modes can be used according to environmental conditions. Among clupeids, gizzard shad, *Dorosoma cepedianum*, apparently change from particulate to filter feeding when, about 25 mm SL (Drenner *et al.*, 1982a). 50 to 70 mm TL alewife, *Alosa pseudoharengus* feed just as well by gulping, filtering and particulate feeding, whereas smaller fish only feed particulately (Janssen, 1976). Adult paddlefish, *Polyodon spathula*, larger than 225 mm SL, are indiscriminate tow-net filter feeders on plankton, while young paddlefish are selective particulate feeders (Rosen & Hales, 1981). Other fishes, when adult retain the ability to use either particulate or filter-feeding modes: such as, the alewife (as mentioned above), the northern anchovy *Engraulis mordax* (Leong & O'Connell, 1969), ciscoes

Coregonus artedii and *C. hoyi* (Janssen, 1978a, 1980).

Dependence on prey composition, size, and density. Switching from particulate to filter-feeding behaviour is a function of various factors, such as: prey density and available prey size range. High prey densities of microcrustaceans (higher than 100000 *Daphnia* m⁻³) elicit filtering in alewives larger than 160 mm TL. Particulate feeding or gulping are used at much lower densities (Janssen, 1978a). Filter-feeding behaviour occurs in 50 to 70 mm TL alewife, when high densities of diatoms (*Tabellaria*) are present. At this size, the fish diet shifts from exclusively zooplankton to phytoplankton, zooplankton, and detritus. High densities of *Daphnia* also induce gulping in ciscoes, but tow-net filtering never occurs even at higher densities (2000000 *Daphnia* m⁻³). Experimentally, Leong & O'Connell (1969) found that high densities of *Artemia salina* nauplii (about 0.6 mm long) elicit filtering in *Engraulis mordax*, but high densities of adult *A. salina* (5–10 mm long) elicit particulate feeding. Small *Tilapia aurea* (40–50 mm SL) use rapid and rhythmic suctions to capture *Bosmina* concentrations caught in the water-surface film (Lazzaro, pers. observ. in aquarium). But, they feed particulately in the water column on evasive copepods. *Sarotherodon galilaeus* use filter-feeding behaviours to capture surface-trapped prey, midwater prey, and prey near the bottom (Drenner *et al.*, 1982c). These authors observed that *S. galilaeus* (20–42 mm SL) switch to filter feeding on remaining nauplii and copepodites, after eliminating, by particulate feeding, the large-sized prey (larger than 0.38 mm), such as *Bosmina*, *Ceriodaphnia*, *Daphanosoma*, and adults of *Mesocyclops*.

Nevertheless, not all high densities of small suspended organisms stimulate a filtering behaviour in obligate filter feeders. As observed by Drenner *et al.* (1982b), dense concentrations of the phytoplankter *Ankistrodesmus* sp. fail to induce the pump filtering behaviour in gizzard shad.

In experimental trials with Northern anchovy, *Engraulis mordax*, O'Connell (1972) observed that, although biting (i.e. particulate feeding) increases with adult *Artemia* density, and filtering with nauplii density, the frequency of response for each corresponding feeding behaviour appears lower at higher densities of the alternative prey type.

Vision versus chemoreception. There is a lack of information concerning the senses used by filter-feeding fish to detect their food. Nevertheless, numerous works demonstrate that filter feeding is a light independent activity. The Baikal omul, *Coregonus autumnalis migratorius*, filter feed when there is not enough light to see its zooplanktonic prey (Volkova, 1973). Thus, the author presumed that the fish taste the prey brought into its mouth (where the taste buds are located) by the respiratory currents, before it induces filter feeding. Holanov & Tash (1978) observed that threadfin shad, *Dorosoma petenense*, filter feed under both light and dark conditions, which suggests also that chemoreception rather than vision induces filter feeding. They proposed chemoreception as a trigger mechanism to stimulate filter feeding. At high light levels, they added brine shrimp nauplii or phytoplankton, which both cause visual changes by colouring the water. In those experimental conditions, the shad begin feeding only after several minutes. They start also filter feeding near a source of water free of any suspended matter, but previously inhabited by zooplankton.

D. Schooling of planktivores

Since schooling prey are better protected against predators than solitary ones (Brock & Riffenburgh, 1960; Neill & Cullen, 1974), foraging filter feeders, as well as particulate feeders, use structured and stable schooling behaviours, in response to predator pressures (i.e., potential or real attacks), when feeding in open water, far from sheltered areas where they remain when not feeding. However, many shallow water zooplanktivores school when feeding in the water column above the substrate where the shelters are abundant (Hobson, 1968). Thus, the differential opportunity for shelter may not be the only selective advantage of schooling (Breder, 1959; Shaw, 1978).

The abundant literature on fish schooling has been summarized by Radakov (1973). The behaviour of schools is well documented in herring, sardinella, mackerel, young Cyprinidae, anchovy, and menhaden. The biological value of schooling is diverse: feeding, defense, reproduction, migration, tolerance of diverse conditions, and others.

The effect of schooling on the feeding success of planktivores, when plankton is patchily distribut-

ed, depends on the nature of the patchiness (Eggers, 1976). But, one selective advantage is obvious: schooling planktivores can explore larger water volumes than solitary planktivores. Because the rate of prey consumption by planktivores is affected by schooling, Eggers (loc. cit.) emphasized (1) the necessity to consider the effects of schooling in assessing food selection by schooled planktivores, and (2) the discrepancy that could result between a predicted diet composition, based on a predator-prey model assuming solitary behaviour of the predator, and data collected from schooled fish. For example, in laboratory experiments, O'Connell (1972) noted a graduation in the feeding response of Northern anchovy, *Engraulis mordax*, within a school: a higher percentage of biting occurred at the front, and a higher percentage of filtering at the rear. Moreover, the variations in the strength and intensity of this gradient were dependent on the relative abundances of the two sizes of prey in the water.

III. Mechanisms of prey selection

To study invertebrate predation, Holling (1966) developed a model of the predation cycle in which he considered the predation-act as a succession of discrete events: prey search, prey encounter, prey pursuit, prey capture, and prey consumption. Each event can be measured experimentally and the predator's success rate at each event is independent of the previous event. This model permits one to study how a predator alters its feeding behaviour in response to prey. A similar approach to Holling's has been used by Ware (1973), Werner & Hall (1974), O'Brien *et al.* (1976), Drenner (1977), Gerritsen & Strickler (1977), Eggers (1977, 1982), Drenner *et al.* (1978), O'Brien (1979), Gibson (1980), and Wright & O'Brien (1984), to study the feeding behaviour of various vertebrate and invertebrate predators. Some of these models are reviewed by O'Brien (1979) (see also section V.A.). The quantitative and qualitative characteristics of the set of prey ingested by a predator by unit of time are determined by the product of the different success rates (one for each event) for each prey type, and corrected for the time used to detect, pursue, capture, and retain a prey. In some cases, differential digestion efficiencies may alter the feeding selectivity of planktivores (see sec-

tions III.A.5. and III.B.3.), and the digestion event has to be considered. In the following, I will use five events for particulate feeders: 1) detection, 2) pursuit (i.e., the attack is decided), 3) capture (i.e., the pursuit is successful and the prey is sucked into the buccal cavity), 4) retention (i.e., the prey, ready to be ingested, is retained on specialized entrainment structures, such as, gill rakers, microbranchiostyles, branchial tooth plates), and 5) digestion (i.e., the prey is attacked by the digestive enzymes); and three events for filter feeders: 1) capture, 2) retention, and 3) digestion.

A. Particulate feeders

1. Prey detection

For successful prey detection, a visual predator is dependent on the optical characteristics of the environment: mainly the contrast in the water (which is determined by the ambient light in the water column), the inherent prey conspicuousness (which is a function of size, shape, pigmentation, contrast, and behaviour), and the visual acuity of the predator (defined by its visual field and its contrast perception). Behavioural and environmental factors control the predator's success rate at each step.

Dependence on light: importance of light contrast for visual predators. Particulate-feeding planktivorous fishes are highly selective on individual food items. Visual feeders are dependent on light to discriminate among prey particles. Selectivity of visual predation is sensitive to light and drops off at low light levels. Suffern (1973), by recording the number of *Daphnia galeata mendotae* eaten by shiners (Cyprinidae) in a given time period and for different light intensities, showed that feeding selectivity of visual predators is light dependent. Although the alewife (*Alosa pseudoharengus*) can feed in the dark, its feeding is 'not selective' (Janssen, 1980): which means that the feeding is not directed at individual prey (i.e., passive prey selection).

Particulate feeding depends on light intensity. Many particulate feeders stop feeding after sunset when natural light intensity is almost zero (less than 0.1 lux for golden shiner, *Notemigonus crysoleucus* (Hall *et al.*, 1970); see also references in

Blaxter (1966)), although field observations attest that bright moonlit nights can provide enough illumination for some feeding. Moonlight feeding ability is described for *Clupea harengus* (Blaxter, loc. cit.), *Oncorhynchus nerka* (Narver, 1970), and *Micropterus salmoides* (Elliot, 1976). *Melaniris chagresi* (Zaret & Suffern, 1976) positively select *Diaptomus gatunensis* during moonlit or starlit nights when the water is calm.

In a recent paper, Gliwicz (in press) shows that in Cahora Bassa Reservoir (lower Zambezi, South East Africa) fluctuations in population densities of four cladoceran species are induced by drastic changes in mortality due to variable predation pressures of Tanganyika sardines, *Limnothrissa miodon*, associated with the lunar cycle. As a consequence of sardines feeding more intensively during full moon than during the new moon and remaining to feed on zooplankton throughout the night, the decreases in densities are more pronounced in less transparent and larger *Daphnia* and *Ceriodaphnia* than in smaller *Diaphanosoma* and *Bosmina*. Moreover, change in feeding intensity with the lunar cycle does not affect eight abundant rotifer species. Gliwicz (loc. cit.) observes that, for a few nights after the full moon, sardines may make use of a 'trap' set up by the timing of the sunset and the moon rise. During nights following the full moon, when one to three hours of complete darkness are followed by the sudden rise of a nearly full moon, zooplankters come close to the water surface and are suddenly exposed to sardines and decimated as soon as the moon rises. At this time feeding rates would be extremely high: from 1.6 to 3.2 captures per second, in conditions of low prey densities (such as, 5 *Bosmina* per liter). Such high feeding rates were observed in *Limnothrissa* laboratory experiments, but only at high prey densities (i.e., 30 *Bosmina* per liter, and 200 *Eudorina* per liter) and under high illumination (daylight). The higher availability of moonlight on nights around the full moon attracting sardines to the offshore area to feed on cladocerans (which are less sensitive to the light of the moon), together with the moon trap allowing sardines for more efficient feeding on cladocerans and copepods (which are more sensitive to the moonlight) may be important in inducing the lunar cycle of zooplankton population densities.

Gliwicz (loc. cit.) emphasizes that, as the moon

trap may be more efficient in the tropics because vertical trajectory of the moon permits more feeding by planktivorous fishes, the lunar cycle may be considered in estimating the abundance of zooplankton. For example, samplings performed with a frequency of a little less or a little more than 28 days would have produced either a gradual decrease (if started just before the full moon) or an increase (if started soon after the first quarter) over several months. Gliwicz suggests that planktonic animals have not yet evolved adaptative strategies to detect the moon trap because of various reasons, such as: 1) the trap set by the timing of the sunset and the moonrise is more difficult to detect, especially, by animals with life span shorter than lunar month, 2) perfectly functioning moon traps are not common, 3) local populations that are adapting to them may be swamped by gene flow from populations that are not experiencing them, and 3) evolution in clones is slow whereas learning in vertebrate predators is fast.

Prey conspicuousness: prey visibility and behaviour. Prey conspicuousness is a function of morphological characteristics, including size, shape, contrast, and pigmentation. It is also influenced by the prey motion behaviour (which modifies the time of direct exposure to the predator) and the light contrast between the prey and its background. Contrast is a major component of underwater prey visibility (Lythgoe, 1968). Both the inherent contrast between differentially pigmented areas of the prey body and the relative contrast between these differentially pigmented areas and the environmental background, contribute to the total visibility of the prey to the predator. For a prey to be conspicuous, its body structures must differ from each other and the background in brightness (i.e., contrast), wavelength distribution (i.e., colors), or both (Levine *et al.*, 1979).

As a consequence of the heavy pigmentation of *Daphnia*'s ephippia (ephippia are sexual eggs of cladocerans and copepods), pumpkinseed sunfish (*Lepomis gibbosus*) and yellow perch (*Perca flavescens*) selectively feed on ephippial over similarly sized non-epippial *D. galeata mendotae* in a Connecticut pond (Mellors, 1975). Moreover, in Lakes Ontario and Erie, Clemens & Bigelow (1922) mentioned that ephippia were abundant in the stomachs of ciscoes (*Leucichthys* spp.). In experi-

ments, 15-spined sticklebacks (*Spinachia spinachia*) prefer darkened mysids (*Neomysis integer* dipped in powdered carbon) to the same body sized light mysids (daylight-adapted) (Kislalioglu & Gibson, 1976).

In marine environments also, more visible prey are selected by planktivores. Jack mackerel (*Trachurus symmetricus*) larvae select preferentially bright coloured organisms, such as the harpacticoid copepod *Microsetella norvegica* (Arthur, 1976). According to Zaret (1980), the conspicuousness of a prey is determined not only by its inherent total visibility (which is mainly influenced by its more visible body part), but also by the range of visual acuities of the fish in the present light conditions of the aquatic environment.

Zaret (1969, 1972b) demonstrated that preferences by *Melaniris chagresi* (Atherinidae) for one of two similar sized-morphs of the cladoceran *Ceriodaphnia cornuta* is highly correlated with the difference in eye diameter pigmentation. The eye of the preferred morph possesses a pigmented area up to 80% larger than that of the other's. As light dependent predators, *Melaniris* see more easily the high contrast of the large black compound eye against the rest of the transparent prey body. Confer & Blades (1975) suggested an alternative explanation for the results of Zaret (loc. cit.) as the density of the preferred large-eyed morph of *C. cornuta* offered to *M. chagresi* was twice the density of the small-eyed morph. Other laboratory experiments using equal initial densities of large-eyed morphs and supereyed (i.e., small-eyed morphs previously fed on a solution of india ink particles develop a greater black pigmentation area behind the eye) showed that *Melaniris* shift their preference towards the small-eyed morphs with supereyes (i.e., the most visible among the two *Ceriodaphnia* morphs) (Zaret, 1972b). As a consequence of changes in fish visual predation intensity, prey of lower inherent contrast (or total visibility) may be favoured against more contrasted ones. For example, many *Daphnia* species produce cyclomorphic morphs less attractive to fish predators. As observed by Zaret (loc. cit.), the reduced compound-eye morphs that are produced, suffer a lower rate of fish predation.

Another example emphasizing the importance of body visibility in prey detection by visual predators was given by Zaret & Kerfoot (1975): studying

Melaniris feeding on *Bosmina longirostris*, they have attempted to separate the respective effects of prey body size and total prey visibility (determined by *Bosmina* eye-pigmentation diameter) on predator electivity. They observed *Melaniris* feeding selectively upon *Bosmina* individuals having the greatest amount of eye pigmentation, and not according to prey size. In this type of situation, size-selective predation appears to be a less important pressure than visibility-selective predation on zooplankton communities. Comparing the relationships between eye-pigmentation diameter, before and after *Melaniris* predation, and body length, the correlation presents both a lower coefficient and a smaller slope after predation. The authors interpreted these results as a selective predation of *Melaniris* according to eye-pigmentation diameter (i.e., the main contrasted area of the prey body). Actually, if *Melaniris* remove large-bodied *Bosmina* (because eye-pigmentation diameter and body length are correlated) as well as, small-bodied, large-eyed *Bosmina*, it results in a larger number of large-bodied, small-eyed *Bosmina* than before, which makes decreasing the strength and the slope of the correlation. However, the eye-pigmentation diameter of *Bosmina* (as well as, *Daphnia*: see Hrbáček (1977)) shows considerable daily photomechanical movements according to the illumination (contraction in light and dilatation in dark) which made Confer *et al.* (1980) discredit some of this eye-size work of Zaret (loc. cit.) which was subsequently rebutted by Kerfoot's (1980) eye-diameter versus pigment-diameter commentaries. Because the fish select the largest and more conspicuous individuals of the prey population, and not only the largest ones, *Melaniris* shows selective predation according to total prey visibility. But, in all situations where the dimensions of the main pigmented area (i.e., the more visible part of the prey body) are highly correlated with body size, the consequence of visual fish predation would be a reduction in the mean body size of the prey population, even if the fish is visibility selective.

Vinyard & O'Brien (1975) have shown that the rate of predation on hemoglobin-containing *D. pulex* is higher than on individuals not containing hemoglobin. Hemoglobin-containing *D. pulex* are not commonly found in lakes: although this species can produce hemoglobin, it is almost always clear. Increased predation on hemoglobin-containing

Daphnia may be the reason why hemoglobin is produced only during stressful situations or in the absence of fish. Hemoglobin production by *Daphnia* was observed by Fox (1948) in ponds normally not containing fishes.

Aspects of prey morphology other than eye pigmentation, have been demonstrated to contribute to total visibility and vulnerability of prey to predators, such as: pigmentation of the mandibles in *Chaoborus obscuripes* (Stenson, 1980), and gut pigmentation from ingested algae in *Daphnia* (Vinyard & O'Brien, 1975). Motion behaviour also contributes to the conspicuousness of prey. Differential vulnerability of cyclopoids and calanoids to predation by planktivores can be analyzed through discriminatory considerations, such as prey motion behaviour (the erratic jumping motion of cyclopoid copepods is more noticeable to visual planktivores than the characteristic gliding motion of calanoids: Brooks, 1968; the saltatory motion of cyclopoids attracts the attention of fish: Confer & Blades, 1975), prey escape ability (calanoids generally escape better than cyclopoids: Confer & Blades, loc. cit.; Vinyard, 1980), prey conspicuousness (stouter bodied cyclopoids are probably more conspicuous than calanoids of the same body size), and fish experience of prey (particulate feeders learn to recognize visually prey, and thus use more vigorous attacks to capture evasive copepods: Vinyard, loc. cit.). So, the calanoid/cyclopoid ratio is usually observed to decrease with increasing predation pressure by visual planktivorous fishes (Hrbáček, 1962; Grygierek, 1962; Brooks & Dodson, 1965; Hrbáček & Novotna-Dvorakova, 1965; Grygierek *et al.*, 1966; Wells, 1970; Hutchinson, 1971; Hillbright-Ilkowska & Weglenska, 1973; Losos & Hetesa, 1973; Lynch, 1979; Hurlbert & Mulla, 1981). Furthermore, in response to predation pressures, prey can develop anti-predatory behavioural patterns to spatially segregate themselves from predators during periods of peak susceptibility (see the abundant literature published on vertical and/or horizontal migrations of zooplankton towards less exposed habitats), or reduce individual prey vulnerability when exposed to predators (patch formation). Together, morphological and behavioural characteristics are responsible for the conspicuousness of zooplankters to visual zooplanktivores.

Visual acuity of fishes: contrast perception and vis-

ual field. The physical and physiological properties of the eyes of fishes determine the effectiveness of their vision underwater. The relevant parameters are: the contrast perception threshold (which is the most important as it limits the maximum visible range of an object), the spectral sensitivities (to discriminate colors), and various measures of acuity (Hemmings, 1974). Recent studies on the nature of fish vision have pointed out the importance of light contrast for prey detection by planktivorous fishes (Hemmings, 1966). Hester (1968) demonstrated that visibility of prey depends mainly on light contrast at all light levels, and only on light contrast at low light levels. Ingle (1971) established that fish visually discriminate between objects on the basis of their size, color, contrast, distance, orientation, and motion.

In experiments upon underwater resolution acuity, Muntz (1974a) emphasized that if hypotheses are to be made about the visual efficiency of fish, spectral sensitivities, acuities and contrast perception thresholds must be known for the species concerned. Contrast perception thresholds for the goldfish (*Carassius auratus*) have been described by Hester (1968), while resolution acuities have been obtained for two pelagic tuna species by Nakamura (1968). Hemmings (1974) suggested that measurements of optical properties of water in which the fish live could demonstrate whether its behaviour is intensivity- or visibility-related.

In a recent paper on the ecological adaptations in fishes' vision, Lythgoe (1979) presented evidence that in underwater environments at natural light conditions, large prey farther from the predator are more visible than closer and smaller ones. He assumed that at wavelengths where the water is more transparent, contrasts for bright close objects may be relatively low, but will reduce less rapidly with distance, until at limits of visibility all (large) objects remain most easily seen. These results draw upon the interpretation of the previous model of 'apparent-size' developed by O'Brien *et al.* (1976) (see section V.A.1.) to describe the selective predation of bluegill sunfish. Their model predicts that when the fish is faced with similar prey of different sizes, the fish selects the apparently largest one. Thus, Lythgoe's paper may provide some help in answering the basic question of distance perception: How do the fish discriminate between a large prey farther away and a small one closer? The fish

should select the most visible prey, i.e., the larger, farther one. It should be added that fish have two eyes and so can control the distance between prey in the space by other means than by apparent-size. A fish is also moving and thus, the image of more distant objects are moving on the retina slower than that of closer objects (Hrbáček, in litt.).

Muntz (1974b), summarizing behavioural data on vision of *Stardinius erythrophthalmus* (Cyprinidae), concluded that contrast thresholds for fish are very important since they determine the greatest range at which objects can be detected. The most visible objects underwater will presumably be large objects that have a high inherent contrast with their background. Smaller objects and objects having low inherent contrast will disappear at much shorter distances. Muntz (loc. cit.) used evolutionary considerations to investigate the adaptative response a predator could develop to see prey more easily, such as: nearer objects brighter than the background, can be best detected by retinal receptors less sensitive to the background (i.e., offset visual pigments; so that the objects appear brighter), while, inversely, intrinsically less visible objects, darker than the background, will be best detected by receptors more sensitive to the background (i.e., matched visual pigments). These arguments are in agreement with Lythgoe's (1968) contrast sensitivity hypothesis for vision under photopic conditions.

Planktivorous fishes, such as the common goldfish, *Carassius auratus* (Cyprinidae), are also able to discriminate among individual moving prey (Protasov, 1968). In a neurophysiological study of trout, Galand & Liege (1975) recorded different types of retinal ganglion cells. Some of which are specialized motion receptors, while others are on-receptors, off-receptors (some of which are directionally sensitive), either spontaneous or continuously activated units. Some ganglion cells have their activity dependent on light intensity, and other large scope units respond to movements. Thus, as previously shown by Ware (1973), a moving prey is more successfully detected by rainbow trout (*Salmo gairdneri*) than a relatively non-moving one. Goldfish also possesses receptors specialized to distinguish between two types of movements which lead to different fish behaviours (Ingle, 1968). Slow background movement induces a swimming behaviour from the fish, while a fast moving object may induce a pursuit and attack behaviour.

So, within the visible range of the fish's vision, motion may increase the conspicuousness of a prey, initiating the response of these specialized retinal photo-receptors.

Janssen (1982) determined that to forage on zooplankton a facultative planktivore, bluegill, uses a hover-search method in the littoral zone, whereas an obligate planktivore, blueback herring, uses a swim-search method in the pelagic coastal areas. He emphasized that the presence of motion detectors as a part of the visual processing system would be detrimental to bluegill in locating prey, because the searching while swimming fish would be falsely stimulated by images of background objects (such as vegetation) moving across its retina. The total search time of a bluegill is partitioned into time actually searching and time moving between search locations. Bluegill searches while stopped (hovering). If a prey is sighted, it swims to it, sucks it in, then coasts to a stop, and searches again. Janssen (*loc. cit.*) suggested that hover-search used by bluegills is adapted to heterogeneous backgrounds where detection of prey motion is important, and swim-search used by herrings is useful where the background is not heterogeneous. In fact, facultative planktivores, such as bluegills, are planktivorous in their juvenile stage. Much of their foraging occurs in the littoral zone where the background is often broken by vegetation, and seston is more prevalent. Works on anurians show that a frog presented with one visual stimulus is not distracted by a second visual stimulus (i.e., the frog attempts to pursue the first prey detected: Pigarev & Zenkin, 1970), because the neurological activity evoked by one prey effectively 'shuts off' the rest of the prey detection system (Didday, 1976). Anurians search stationary and do not move their eyes, as any eye or body movement may inhibit the detection of movement (Muntz, 1977). The prey detection system of a frog is deactivated during jumps while other visual processing systems remain active (Pigarev *et al.*, 1971). Blueback herring possesses visual motion detectors to discern the movements of prey and non-prey moving across the retina, until the prey is directly in front of the fish. But, as blueback herring searches above its swimming track (Janssen, 1981) the prey is never directly in front of the fish, until at final, the fish swims up to take it. Thus, motion may be unimportant for the detection of prey by a swimming fish, and con-

sequently, the fish must rely on other cues to distinguish prey from seston.

The detection rate for each prey species is determined by both the concentration of the concerned prey in the environment and the volume searched by the predator. The volume visually searched by a particulate feeder per unit of time (i.e., the reactive field volume) is a portion of its visual field. The importance of the volume searched for feeding in relation to the visual field increases with increasing fish swimming speed. The lateral position of the fish's eyes determined the visual field, which is nearly spherical in most teleosts (Bond, 1979). However, because of the elliptical shape of the retina, relatively distant lateral objects are in focus, while close objects are not, and near anterior objects in the binocular field are in better focus than more distant objects (Tamura, 1957). Although all fishes do not have equal accommodation abilities to distant vision, these two regions of the visual field (mono- and binocular regions) are used differentially during the predation-act. The relatively distant lateral (and monocular) vision is used mainly to detect prey (or predators), and then, the near sharp (and binocular) vision is used to pursue and capture prey (Protasov, 1968). Vinyard & O'Brien (1976) found that bluegill reactive distance (i.e., the distance at which a prey can be seen by the fish) decreases with decreasing light intensity or increasing turbidity (see Fig. 1). They showed that at high turbidities and/or low light intensities the reactive distance becomes nearly independent of prey size. The same result was predicted by the model developed by Eggers (1977): reactive distances are independent of prey size or shape if the inherent contrast of the prey object is low, if turbidity is high, or if light intensity is low. The shape and size of the visual field explored by a fish during the detection step (i.e., the reactive field volume) can be estimated by measuring the reactive distances (i.e., the maximum distances), and corresponding angular directions, at which a specific prey item is detected (see section V.A.1. on models of prey selection). Generally, the detection of an elusive prey elicits an S-shaped movement from the fish.

2. Prey pursuit

Dependence on prey size, distribution, and density. At low prey densities fish feed in a rather non-

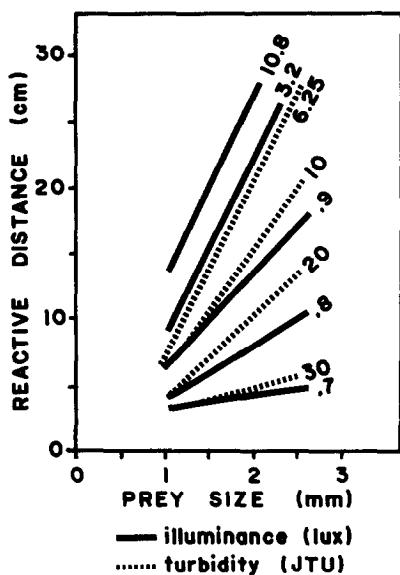


Fig. 1. Relationships between reactive distance of bluegill, *Lepomis macrochirus* (Centrarchidae) and prey size for different illuminances (dotted lines, in lux units) at low turbidity (1 JTU), and for different turbidities (continuous lines, in JTU units) at a constant illuminance (34.9 lux) (from Vinyard & O'Brien, 1976).

selective manner on different prey types (and sizes): each prey detected is pursued and eaten. At higher prey densities fish concentrate on the largest prey sizes (Ivlev, 1961). In laboratory feeding experiments, Brooks (1968) showed the preferential removal of the largest adult-size class of *Diaptomus*

minutus by captive alewives (cyclopoids were not present). Werner & Hall (1974), in similar laboratory feeding experiments, provided identical results using juvenile bluegills feeding upon different size categories of the cladoceran *D. magna*. They demonstrated that planktivore preference is proportional to prey body size, and that the fish begin to feed significantly on the smaller size categories only after the decline in abundance of the larger preferred prey size categories (see Fig. 2).

Dependence on fish hunger. The mechanisms of food intake regulation are not completely known. However, it is admitted that the feeding in vertebrates is controlled by instantaneous signals sent from stretch receptors in the gut musculature to the central nervous system (Hamilton, 1965). Feeding rates and stomach fullness tend to be inversely related. In laboratory trials with rainbow trout (*Salmo gairdneri*) deprived of food for 48 hours, Ware (1972) determined that (1) the pursuit rate on two Amphipoda species decreases significantly with decreasing fish hunger and prey density, and (2) the handling time of prey (i.e., the amount of time necessary to pursue and capture an individual prey, which is equal to the inverse of the maximum feeding rate) increases progressively when approaching satiation. Ware (loc. cit.) emphasized that the rate of prey pursuit by visual planktivores is not proportional to the prey density because a certain time (which duration is dependent upon the internal nutritional state of the fish) is required to

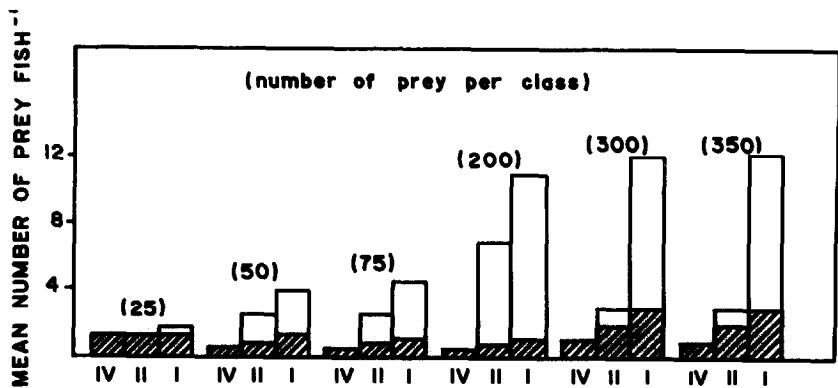


Fig. 2. Mean number of each size class of *Daphnia magna* eaten per *Lepomis macrochirus* (Centrarchidae) for experiments at different prey per class densities (class IV: 1.4 + 0.05 mm, class II: 2.5 + 0.07 mm, class I: 3.6 + 0.05 mm). The striped areas represent the expected numbers in stomach if items are eaten as encountered (computed from the visual field ratios): deviations from the expected show that positive selection is increasing as a function of prey density (from Werner & Hall, 1974).

handle each prey item attacked (see a discussion about the role of handling on the rate of prey consumption in Holling, 1966).

Dependence on fish experience of prey. To explain the selective interest of predators for certain prey types, a learning mechanism to discriminate among prey types (and acquired by previous encounter with the prey) has been suggested by Tinbergen (1960) and called the 'searching images concept'. Rosenthal & Hempel (1970) proposed this mechanism to account for the selective feeding of herring larvae (*Clupea harengus*) on one prey type. This concept was used by Ware (1971) to describe the feeding behaviour changes of rainbow trout (*Salmo gairdneri*) after repeated exposures to palatable food. He observed substantial improvements in the reactive distance of an experienced fish for a familiar food. Moreover, trout may require several days of experience to transfer this learning to new prey, rather than the familiar one. Vinyard (1980) tested the ability of bluegill sunfish to modify its pursuit choice when encountering two distinct prey types. He demonstrated that the fish can use the information concerning the prey size and escape ability. Bluegill displays differential capture behaviours according to the prey type detected. During laboratory feeding trials, bluegill discriminates between copepod and cladoceran, using active and vigorous motions to capture *Diaptomus pallidus* and comparatively leisure ones to capture *Daphnia pulex*. Vinyard (loc. cit.) attributed this shift to a learning process based on the formation of searching images of the prey (Tinbergen, loc. cit.). Thus, in particulate feeders, the previous experience of the fish for different prey types may alter, not only the pursuit choice (if prey are detected simultaneously), but also the capture success (Confer & Blades, 1975; see section III.A.3. and V.A.1.).

3. Prey capture

The capture success rate of planktivorous fishes depends on both the capture efficiency of the predator and the escape ability of the prey.

Gape limitation of larvae and small species. Planktivorous fishes (sensu Zaret, 1980) are ranked among 'gape-limited predators' (G.L.P.) when their mouth diameter, or gape, limits the maximum size

of an intact prey they can swallow. Because of the small size of their mouths, the youngest fishes initially select small zooplankton. During growth, they feed progressively upon larger prey. This maximum size selection imposed by the fish's gape is well documented for young yellow perch (*Perca flavescens*, see Fig.3) by Wong & Ward (1972), for juvenile chum salmon (*Oncorhynchus keta*) by Feller & Kaczynski (1975), for perch fry (*Perca fluviatilis*) by Furnass (1979), and for herring larvae (*Clupea harengus* L.) by Blaxter (1966) and Rosenthal & Hempel (1970).

It is only during a brief period that larval fishes select positively the smallest and less evasive species of zooplankton, and also, the smallest individuals of a single species. The time duration of this gape limitation is brief, and larvae are able to feed on the maximum available prey size within three to four weeks of hatching (Rosenthal & Hempel, loc. cit.; Wong & Ward, loc. cit.; Guma'a, 1978; Hunter, 1979). But, other factors such as the structure and the motion reaction of prey, may result in an important discrepancy between prey size and predator gape (Hartman, 1958). Young marine and freshwater fish larvae have a highly inefficient feeding behaviour and poor visual acuity. Food organisms are most frequently perceived at very short dis-

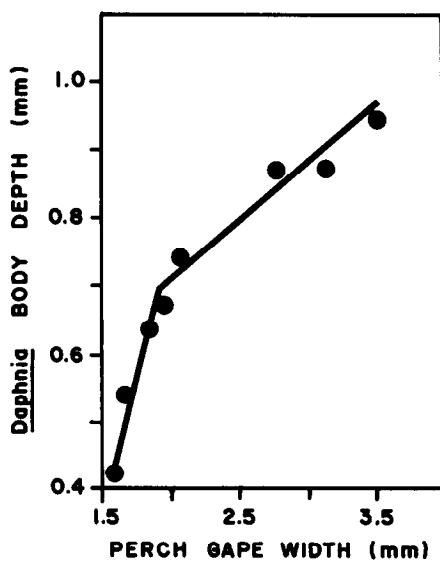


Fig. 3. Relation between yellow perch (*Perca flavescens*) fry mouth gape width and body depth of *Daphnia pulicaria* found in perch stomachs ($n = 771$) of West Blue Lake (Manitoba) during the summer of 1969 (from Wong & Ward, 1972).

tances (from 2 to 8 mm for yolk-sac herring larvae, and from 3 to 40 mm for 15–20 mm herring larvae), and most of them are not successfully captured because of low velocity and poor aiming of the fish. Fish larvae attain more than 50% of feeding success after an average of four weeks of hatching, because of the process of learning, the development of fins (faster darting), and the growth of lower jaws (Rosenthal & Hempel, loc. cit.).

Similarly, some obligate zooplanktivore species of which individuals are smaller than 7–8 cm long are ineffective in capturing the largest individual zooplankters present in the aquatic environment. For example, a 4 cm long guppy, *Poecilia reticulata*, is unable to catch a 5 mm long *D. magna* (Pourriot, pers. commun.). Because of the smaller diameter of the fish mouth, the reduced volume of its buccal cavity, and the resulting weak suction strength and poor aiming, the maximum size of prey items which can be captured intact is limited.

Capture efficiency: effects of experience and mouth structure. Particulate-feeding planktivores use a suction process to capture individual prey items. The intake current is created by an expansion of the buccal cavity. Obligate planktivores (such as whitefish, alewives, smelt) have rounded mouths to produce greater suction speeds. Facultative planktivores (such as salmonids), more adapted to capture larger prey, have large notched mouths. The capture efficiency of planktivorous fishes depends on their previous experience and the prey type (Ware, 1971, 1972; Confer & Blades, 1975; Janssen, 1978a; Vinyard *et al.*, 1982). By learning to recognize prey items, principally according to their motion behaviour, plantivores may improve their capture success, as demonstrated by Beukema (1968) for three-spined stickleback (*Gasterosteus aculeatus*). Beukema's studies support the searching image concept reviewed by Tinbergen (1960). As concluded by Ware (1972), learning to recognize prey is a positive feedback to improve the capture efficiency of vertebrate predators.

While particulate feeding is used by alewives (*Alosa pseudoharengus*) and ciscoes (*Coregonus artedii*) to capture weak zooplanktonic swimmers (such as, cladocerans, cyclopoid copepods, and swimming amphipods), a specialized particulate feeding mode, named 'darting' by Janssen (1978a), is employed to capture evasive zooplankters, such

as calanoid copepods, and *Mysis*. Copepods possess mechanoreceptors which register hydrodynamic disturbances. When darting fishes move rapidly to the prey (from about 1–2 cm distance) while sucking, they eliminate any suction current that stationary sucking would cause. In the same fashion, the small lake trout (*Salvelinus namaycush*) is able to improve its suction abilities by increasing its sucking intake to capture copepods over daphnids (Kettle & O'Brien, 1978). When feeding on *Daphnia*, bluegill rushes to a prey, brakes momentarily while sucking it in, and then shifts towards the next item (Werner, 1977). Alewives and ciscoes open wider their mouths to capture larger prey (Janssen, 1978a), so their covered mouth sides form a suction tube which eliminates lateral leakage and makes the suction more directed.

From experimental works on mechanisms of water flow production over the fish gills, three major concepts have emerged: (1) the water flow over the gills is relatively continuous with perhaps a brief period of low or zero flow, (2) the gills form a significant resistance to flow (Hughes, 1965, 1976; Shelton, 1970; Hughes & Morgan, 1973; Jones & Schwarzseld, 1974), and (3) a 'double-pump' mechanism involving a buccal force pump and an opercular suction pump is responsible for moving water over the gills. Suction feeding in teleosts fishes is a highly dynamic process lasting only 20–100 ms, involving large accelerations, and producing a single rapid pulse of water through the mouth cavity (Lauder, 1980a). Besides technical difficulties associated with measuring rapidly fluctuating pressures, attempts to understand the hydrodynamic aspects of teleosts feeding have relied heavily on concepts borrowed from studies of fish respiration (Lauder, 1980b).

A first theoretical model of suction feeding has been outlined by Osse & Muller (1980) and Muller *et al.* (1982). In this model, the gill bars and filaments are not included (in contrast to models of fish respiration: Hughes & Woakes, 1970) and the operculum plays a decisive role in generating 'both' buccal and opercular cavity negative pressures. Performing experimental tests of the feeding mechanism in bluegill sunfish, Lauder (1983) refuted this previous model and demonstrated an alternative hydrodynamic model of high-speed suction-feeding processes in fishes. He showed that buccal pressures always exceed opercular pressures, as, in nor-

mal bluegills feeding by high-speed inertial suction, opercular pressures reach a maximum of about -120 mmHg, whereas buccal pressures attain values of -500 mmHg. These large negative pressures are achieved only during very rapid strikes at elusive prey. Lauder's results indicate unambiguously that (1) the gill bars function as a resistant element within the mouth cavity (and not the gill filaments of the primary and secondary lamellae as during respiration), and (2) the abduction of the operculum by the dilatator operculi plays little role in generating negative mouth cavity pressures. Lauder (loc. cit.) emphasized that these conclusions on gill resistance apply mainly to fishes feeding by high-speed suction using extremely unsteady flows, (2) species that use body velocity to overtake prey (for example, tow-net filter feeders) will probably exhibit a somewhat different pattern of buccal and opercular cavity pressure changes, and (3) only high-speed suction-feeding fishes and fishes using a slow to moderate approach velocity are likely to exhibit large pressure differentials across the gills. For example, pike (*Esox*) which utilizes rapid accelerations from rest and large amplitude movements during prey capture (Webb & Skadsen, 1980), opens its mouth well before the prey is reached, maintains its mouth and operculums abducted at near maximum level till the final stages of the strike, and possesses long and slender gill bars which do not lie snugly against each other in the abducted position. Thus, during prey capture by *Esox*, no pressure differential exists across the gills. In contrast, bluegill has much slower attack velocity ($5-40$ cm s $^{-1}$) and produces the highest pressure differentials. In the normal rest position during quiet respiration, only a small opening is present between each pair of gill bars, whereas in the early stages of suction feeding, the gill bars are abducted as the gill cover and suspensorium move medially (Lauder, 1980a). Finally, Lauder (1983) stressed that (1) buccal pressures in all high-speed suction-feeding fishes studied to date exceed opercular pressures, and (2) predictions based on current mathematical models of feeding mechanism (at least for rapid prey capture by inertial suction, and despite adjustments by assuming relevant biological constraints) fail to characterize, even generally, the relative magnitudes and waveforms of pressures measured experimentally.

Since visual predators can increase their capture

efficiency by learning to recognize mobile prey and altering their feeding mechanics (for example, prey sucked in at a closer distance, water intake speed increased, as well as other adaptative behaviours), the prey escape ability is only a secondary determinant affecting the selectivity of particulate feeders for zooplankton (Confer & Blades, 1975; Vinyard, 1980). But, it is determinant in controlling the array of prey ingested by filter feeders (Starostka & Applegate, 1970; Drenner *et al.*, 1978; see section III.B.1.).

Modelling the relative capture frequency of zooplankton by visual-feeding pumpkinseed (*Lepomis gibbosus*), Confer & Blades (1975; see section V.A.1.) observed that: (1) when *Lepomis* was fed *Daphnia* for several days and then copepods, the initial capture success for copepods (i.e., the ratio of the number of prey ingested to the number of prey pursued) was low, (2) the capture success of copepods varied daily, probably following rapid fish learning and forgetting, (3) some species of copepods were highly successful at eluding the fish capture (for example, they reported capture success of 79% and 39% for *Diaptomus sicilis* and *D. ashlandi*, respectively), and (4) the capture success of several species of *Daphnia* was nearly 100%. Emphasizing the extremely dynamic capture of particulate feeders for evasive copepods, the authors assumed that no single value was entirely satisfactory, and used an 80% approximation (i.e., the average capture success for six dates).

4. Prey retention

Many works have emphasized the discrepancy between the size of the smallest prey ingested by particulate feeders and the minimum spacing between their gill rakers (Galbraith, 1967; Kliewer, 1970; Seghers, 1975). The role of the retention event in the prey selection of particulate feeders remains often unclear. Theoretically, the retention probabilities of the branchial filters are determined by the cumulative frequency distribution of interraker spacings. If true, the passive sieving mechanism (generally assumed to be the dominant mechanism in biological filters) can be tested by comparing this distribution with the size distribution of the ingested prey.

The attack of particulate feeders is directed at individual prey, but more than one prey may be in-

gested at a time (Wright *et al.*, 1983). Small bodied prey with poor evasive capability are often ingested incidentally through passive selection (determined by the mesh size of the filter). The probability of incidentally ingested prey increases with increasing prey density in the environment. In order to examine the filtering process of particulate feeders, Wright *et al.* (loc. cit.) trained white crappies (*Pomoxis annularis*) to attack preferentially large bodied *D. magna* when presented with dense assemblages of small zooplankton. Small prey, ingested incidentally during the active directed ingestion of individual *D. magna*, are assumed to be included into the diet solely by retention on the gill rakers. The authors observed experimentally that white crappies do not ingest small non-evasive *Ceriodaphnia* sp. in the proportion of their densities in the pool. The retention probabilities determined from the cumulative frequency of the interraker spacings on the first arch disagree with those determined by incidental ingestion estimates (computed, versus prey size, as the ratio of the average percent per 0.04 mm prey size category in the stomach divided by the corresponding value in the experimental pool). Both retention probabilities are sigmoid functions increasing with prey size, but the curves of incidental ingestion and interraker spacings reach a 100% retention success for *Ceriodaphnia* sp. at different prey sizes (0.70 mm and 0.24 mm, respectively). Although some experimental biases were mentioned by the authors, such as: (1) the interraker spacing estimates may have significantly overestimated the actual retention probabilities, as the interraker spacings increase with the degree of buccal cavity expansion, (2) the first arch may not be the main functional retention site for prey, and (3) individual prey smaller than 0.24 mm were not tested in the experiments, Wright *et al.* (loc. cit.) came to the conclusions that: (1) interraker spacing measurements are seriously biased, fail to estimate the actual retention capability of the branchial filter, and should be interpreted with great caution, and (2) the retention process appears to be more dynamic than a simple passive sieving mechanism (but see Drenner *et al.*, 1984a).

From these results it can be emphasized that incidental ingestion may not be a main contributor to the feeding selectivity of particulate feeders, except when (1) small bodied and poorly evasive prey are present at high densities or distributed in a clumpy

pattern, and (2) the largest and most selected prey have low evasion ability, as some attacks may be directed at other smaller prey.

5. Prey digestion: resistance of zooplankton to fish digestion processes

Some zooplanktonic or phytoplanktonic organisms can pass undigested through the gut of planktivorous fishes, and survive when released from the fecal pellets in the environment, escaping predation. Moreover, in the presence of high levels of predation pressure, survival through resistance to digestive processes may have another adaptative value: it is a possible means of prey dispersal which results in an evolutionary trend towards prey populations dominated by especially resistant individuals.

The digestion efficiency for a specific zooplanktoner in a fish gut depends upon the composition of the gastric juices (presence of effective enzymes), the transit time, and the composition of the zooplanktoner's cuticle. Zooplanktonic organisms are generally easily and quickly digested by planktivorous fishes (Gannon, 1976). Nevertheless, prey survival after ingestion by fish can occur among some zooplanktonic groups.

Pumpkinseed sunfish and yellow perch feed selectively on (darker and more conspicuous) ephippial *D. galeata mendotae*, over similarly sized non-ephippial *D. galeata mendotae* (Mellors, 1975; see section III.A.1.). Mellors (loc. cit.) observed that some ephippial eggs of *D. galeata mendotae* can survive the ingestion and the passage through the fish gut. But the percentages of hatch and overall egg survival remain low (smaller than 15%). Although ephippium production increases the vulnerability of *Daphnia* to fish visual predation, the survival of ephippial eggs after the passage through the predator gut appears to reduce the consequences of their selective capture. Nevertheless, it may be noted that ephippia and other longevity eggs are not organisms, but resistance forms.

However ostracods do not belong strickly to plankton, but to benthos, Vinyard (1979) found that 26% of the ostracods *Cypriodopsis vidua* ingested by small bluegill sunfish (39–59 mm SL) survived the passage through the fish gut, and appeared undamaged and fully active in the feces. Moreover, 24% of rejected dead ostracods did not

show net evidence of digestion. Since ostracods may occasionally reach high population densities (Sandberg, 1964), the high percentage of surviving ostracods has wide implications relative of both prey and predator. For example, Ivlev (1961) observed only a significantly negative electivity for the ostracod *Cypris* sp. when fed, together with *Daphnia*, *Bosmina*, and *Diaptomus*, to bleak (*Alburnus alburnus*), and Vinyard (1979) noted occasional rejections of ostracods by bluegill. Fish avoidance of ostracods when alternate prey are simultaneously available may be the result of a learning process. Since the fish expends energy in the capture of the prey and receives no energy in return through assimilation, the fish may learn to recognize and avoid such undesirable prey organisms.

Another mechanism which reduces the fish digestion efficiency has been suggested by Vinyard (loc. cit.). High total ingestion rates, which occur in the presence of dense prey populations (or in environments rich in suspended matter), and the consecutive rapid passage through the fish gut (due to reduced transit times) may result in high survival rates of ingested prey.

Studying brook charr (*Salvelinus fontinalis*) predation on *Cyclops abyssorum tetricus* copepodites (IV and V) and adults in oligotrophic Lake Zielony (Tatra Mountains, Southern Poland), Dawidowicz & Gliwicz (1983) observed that a) egg-carrying females were highly selected over egg-free females, males and copepodites, but b) removal from the lake of most copepodites and adults of *C. a. tetricus* by charr, instead of causing serious damages to the *Cyclops* population, rather favoured it. Gliwicz & Rowan (1984) showed that the higher survival rate of *Cyclops* eggs and nauplii (60%) despite heavy predation by charr on egg-carrying females was a natural consequence of *Cyclops* eggs passing unharmed through the charr guts (as eggs from the lake and from the rear part of the charr gut hatched in similar proportions). The eggs defecated by charr sink to the surface of the bottom sediments where they continue their development. As the newly hatched nauplii are not fed upon by their cannibalistic parents (because adults are already removed by charr), the new generations persist in the lake in high density till they reproduce next April–May. This may explain why nauplii densities increase after the extinction of egg-carrying females

in May–June. Dawidowicz & Gliwicz (loc. cit.) emphasized that resistance of crustacean sexual eggs, including ephydrial eggs of cladocerans (Mellors, 1975) to fish digestion processes may not be only an important adaptation to escape predation by planktivorous fishes, but also an adaptation which favors the fish themselves, since their planktonic food resources do not become overexploited. These authors wondered to what extent this phenomenon may be considered as a co-evolutive process.

B. Filter feeders

Contrasting with the well-documented size-selective impact of particulate-feeding fish, there is a lack of information concerning the selective ingestion of plankton by limnetic filter-feeding fish and the dynamics of plankton communities in response to these fishes. Filter-feeding fish feed on plankton by engulfing or sucking a certain volume of water containing prey items into the buccal cavity (see section II.B.). Their feeding behaviour is not visually directed at individual prey, and therefore, filter-feeding fish may capture more than one prey at a time. Prey are encountered in proportion to their densities in the water, and captured according to both the differential escape abilities of the prey items, and the capture efficiency of the fish which is dependent upon the feeding behaviour displayed (Drenner *et al.*, 1978, 1984a). Because the detection and pursuit events cannot cause selectivity, the predation-act of filter feeders is reduced to only three successive events: 1) capture, 2) retention, and 3) digestion.

1. Prey capture: a determining event for zooplankton ingestion

Live zooplankters are able to evade suction generated currents. To estimate the direct escape response of different zooplankter species, Drenner *et al.* (1978) and Drenner & McComas (1980) used a simulated fish-suction intake (Drenner, 1977; Drenner *et al.*, 1978) and measured specific capture probabilities. The capture probabilities (Drenner, 1977; see Fig. 4) were highest for the cladocerans *C. reticulata* (96%), *D. galeata mendotae* (92%) and *D. pulex* (76%), intermediate for *Diaphanosoma brachyurum* (49%), *Mesocyclops* spp. (28%) and

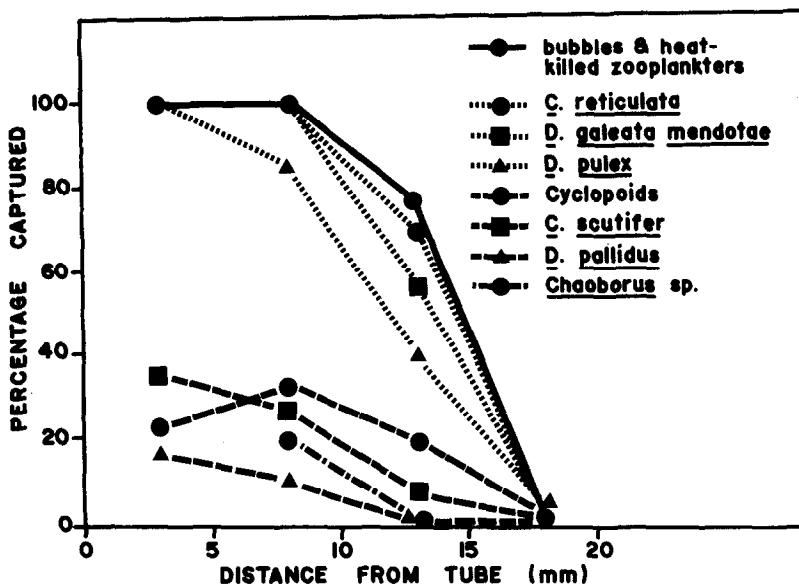


Fig. 4. Percent of particles and organisms captured by the siphon system versus their distance from the tube. The points plotted at distance 3, 8, 13, and 18 mm represent averages of capture frequency (i.e. success) within the intervals of 1 to 5 mm, 6 to 10 mm, 11 to 15 mm, and 16 to 20 mm, respectively. The conditional probabilities mentioned in the text for live zooplankter are the ratio between the areas under the frequency curves for the live zooplankter and the non-motile bubbles and dead zooplankters (from Drenner, 1977).

Cyclops scutifex (24%), and lowest for *Diaptomus pallidus* (7%) and *Chaoborus* sp. (9%). Thus, cladocerans are more vulnerable than copepods to the suction capture mechanism of filter-feeding planktivores. These results confirm the previous laboratory experiments performed by Szlauer (1965) using a glass-tube device. He showed that adult copepods have the highest ability to escape, while the cladoceran *B. longirostris* has a null escape ability. Because algae have no escape mechanisms, filter-feeding fish require no specific capture strategies to utilize them as food. Therefore, only the retention efficiency determines the selectivity for motionless particles, such as, phytoplanktonic cells or colonies. They are passively engulfed into the fish buccal cavity, captured in proportion to their density in the environment, and ingested only according to the feeding rates of the fish for the different available sizes (i.e., passive selectivity).

Tow-net filter feeders. Although large zooplankters, mostly copepods, detect and avoid filter devices used to capture plankton, i.e., net, and pump (Flemminger & Clutter, 1965; Drenner & McComas, 1980), tow-net filter feeders effectively capture large evasive zooplankters. Experimentally,

Flemminger & Clutter (loc. cit.) studied the avoidance mechanisms used by populations of zooplankton to towed-nets. They concluded that: (1) zooplankters can avoid the capture by nets, because both visual and hydrostatic pressure disturbances are detected, (2) the avoidance tends to be less in denser populations, because interindividual interferences may restrict the escape movements of zooplankters, (3) the light intensity has no apparent effect on the avoidance efficiency of copepods, because, although capable of light perception, they probably cannot form images, (4) the apparent avoidance efficiency differs among copepod species (for example, *Acartia tonsa* is more easily sampled than *A. clausi*), and (5) copepods are capable of directed movements of escaping (for example, *Labidocera acutifrons* can display directed movements at a speed of 80 cm per second, i.e., 230 body lengths per second, over more than 15 cm). But, direct observations of feeding mechanisms (using high speed motion pictures, video recordings, or SCUBA equipments) as well as indirect evidence (given by functional morphology studies of the feeding apparatus, and stomach content analysis: see also section III.B.2.) clearly demonstrate the efficiency of tow-net filter feeders (compared to the

low capability of towed nets) in capturing large evasive zooplankters. The Atlantic menhaden (see Fig. 5B) use high swimming speed (2.0–2.5 body lengths per second) with wide mouth opening to graze at high rates on adult *Acartia tonsa* (1.2 mm

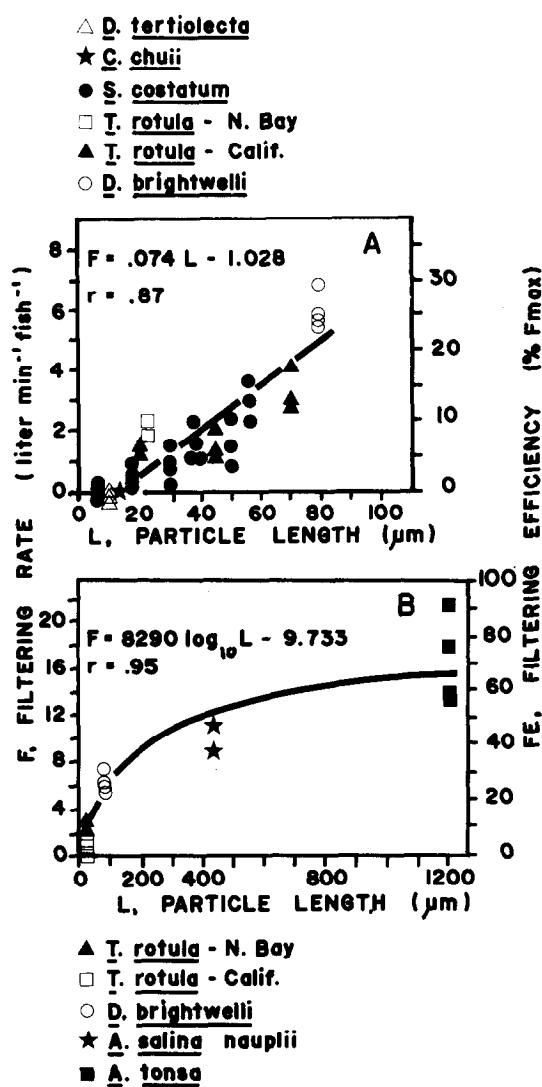


Fig. 5. Grazing of *Brevoortia tyrannus* (Clupeidae) (A) on 5 species of phytoplankton as a function of increasing size or chain length (0.1 μm *Dunaliella tertiolecta*, 13.2 μm *Carteria chuii*, 7.8–55.6 μm *Skeletonema costatum*, 21.6 μm *Thalassiosira rotula* (Narragansett Bay) and 19.0–70.3 μm *T. rotula* (California clone), and 79 μm *Ditylum brightwelli*, and (B) on regularly shaped phytoplankton (79 μm *D. brightwelli* and 19.0 μm single cells of *T. rotula*), *Artemia salina* (430 μm long), and *Acartia tonsa* (1200 μm long) as a function of length (from Durbin & Durbin, 1975).

long) and *Artemia salina* nauplii (0.4 mm long) (Durbin & Durbin, 1975). Paddlefish, *Polyodon spathula*, swims slower and strains food from the water column over their gill rakers: *Daphnia* and calanoid copepods represent 75% of the volume of the food ingested in the stomach (Rosen & Hales, 1981). Using an artificial pump device, Janssen (1976) demonstrated that sucking while moving at the prey is more effective than sucking while stationary to capture calanoid copepods.

Walters (1966), using high speed motion pictures, studied the mechanisms of filter feeding in the scombrid wavyback skipjack, *Euthynnus affinis*, swimming rapidly (5.9 body lengths per second) with its mouth widely opened when feeding. The rate of expansion of the orobranchial chamber was not rapid enough to produce a noticeable water flow in through the mouth. Walters also observed that a 4 cm piece of Osmeridae, used as food, was not forced ahead or laterally, by the rapid approach of the fish mouth opening. Moreover, when the mouth was opened the drag of the fish was not altered because the size of the gill openings remained constant during swimming. Thus, Walters concluded that the fish swam over its prey rather than sucked it in. Another scombrid, *Rastrelliger kanagurta* feeds with its mouth opened widely and its branchial apparatus expanded nearly at its maximum (during up to several minutes), while swimming rapidly. Using SCUBA equipment, Colin (1976) observed this scombrid feeding in that manner on freshly released eggs (0.6 mm in diameter) of Labridae *Thallasoma* sp. Tow-net filter-feeding behaviours have also been described in another scombrid: *Scomber japonicus* (O'Connell & Zweifel, 1972), among Clupeidae: *Alosa pseudoharengus* (Janssen, 1976, 1980), *Brevoortia tyrannus* (Durbin & Durbin, 1975), *Sardinops caerulea* (Nelson, 1979), in Engraulidae: *Engraulis mordax* (O'Connell, 1972), and in Coregonidae: *Coregonus artedii* and *C. hoyi* (Janssen, 1978a, 1980). Tow-net filtration has been suggested for the clupeid *Ethmalosa fimbriata* from stomach content analyses, but direct observations are lacking (Fagade & Olanyan, 1972; Lazzaro, unpubl. data). Most of these fishes are pelagic schooling marine (in origin, at least) planktivores: this may have something to do with the predominance of calanoids at sea (Janssen, in litt.).

Pump filter feeders. Pump filter feeders use rhythmic suctions, not directed at individual prey, to capture suspended organisms. Periodical unusual swallowing movements, probably related to the movement of food particles from the entrapment structures (gill rakers, microbranchiospines, pharyngeal teeth or pockets) towards the oesophagus, interrupt the pumping sequences of the feeding (Drenner *et al.*, 1982b). Few studies have been done on the functioning of the capture event in pump filter feeders, except in Clupeidae: *Alosa pseudoharengus* (Janssen, 1978a, 1978b, 1980), *Dorosoma cepedianum* (Drenner, 1977; Drenner & McComas, 1980; Drenner *et al.*, 1982a, 1982b), *Dorosoma petenense* (Holanov & Tash, 1978), in Cichlidae: *Sarotherodon galilaeum* (Gophen *et al.*, 1983b), *Haplochromis nigripinnis* (Moriarty *et al.*, 1973), in Coregonidae: *Coregonus hoyii* and *C. artedii* (Janssen, 1978a, 1980), and in Mochokidae: *Brachysynodontis batensoda* (Lauzanne, 1970, 1977; Im, 1977).

The capture efficiency of pump filter feeders for zooplankton only depends on the differential escape responses of prey species. Since their suctions are not directed at individual organisms, their sucking intake cannot be improved according to prey types (whereas that of particulate feeders can: see also section III.A.3.). In contrast to tow-net filter feeders, pump filter feeders, which create pressure disturbances when sucking in the water surrounding the prey items, are poorly efficient in capturing large evasive zooplankters (Starostka & Applegate, 1970; Drenner *et al.*, 1978; Drenner & McComas, 1980). In laboratory feeding trials, Drenner *et al.* (1982c) demonstrated that pump filter-feeding *Sarotherodon galilaeus* have feeding selectivities increasing with prey capture success. The selectivities were significantly higher for *Ceriodaphnia reticulata*, *Bosmina longirostris*, *Diaphanosoma brachyurum* and *Mesocyclops leuckarti* nauplii, and lower for *Mesocyclops* copepodites and adults. In similar trials, Gophen *et al.* (1983b), showed that pump filter-feeding blue tilapia, *T. aurea*, are escape-selective predators on zooplankton, selectively feeding on non-evasive prey, such as *Bosmina* sp. and *Ceriodaphnia* sp., over more evasive prey, such as *Thermocyclops* sp. copepodites and adults.

In summary, (1) tow-net filter feeders are less sensitive than pump filter feeders to the escape ability of prey, tow-net filter feeders are more effective

than pump filter feeders in capturing adult calanoid copepods, 3) tow-net filter feeding is probably a rather non-selective feeding mode (Janssen, 1976; see Fig. 6; Rosen & Hales, 1981), and (4) selectivity of pump filter feeders is based on prey escape ability and mechanical retention efficiency of their filters, whereas selectivity of particulate feeders is principally based on prey detection and pursuit since, generally, they capture pursued prey with high success rates.

2. Particle retention: a determining event for motionless particle ingestion

The feeding selectivity of filter feeders for motionless particles (phytoplankton, and microzooplankton, such as protozoans) is governed by their retention capabilities which depend on both the structure and the functioning of their

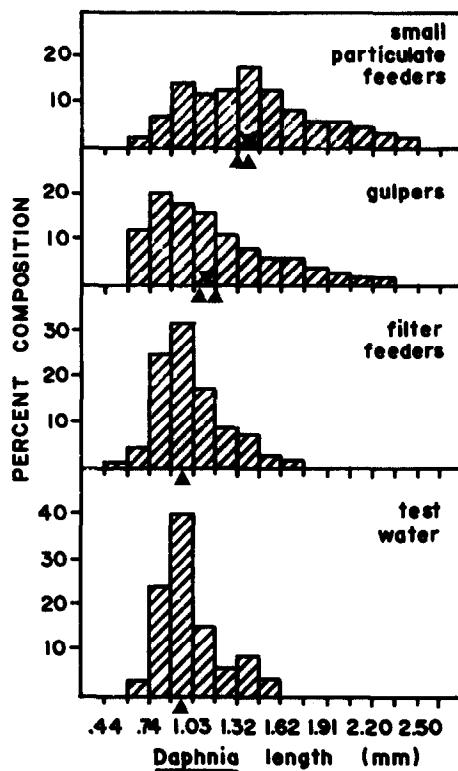


Fig. 6. Daphnia length distribution in test water and *Alosa pseudoharengus* (Clupeidae) stomachs of various feeding modes. Arrows denote median prey size for fish: particulate feeders are highly size selective, gulpers are less, and filterers are not (from Janssen, 1976).

branchial filtering apparatus. For a long time, filter feeding in fishes has been considered as a simplistic sieving mechanism, during which particles too large to pass through the spacings of the filtering mesh are retained. In most fishes, the filtering mesh is primarily represented by the gill rakers structure, which is particularly complex in Clupeidae and Coregonidae (Monod, 1949). The gill rakers are set on the anterior part of the gill arches which constitute the elements of the branchial basket. In other fishes, such as Cichlidae and Citharinidae, microbranchiospines are organized in a filtering band along a groove located on the internal and/or external part of some or all gill arches, just above the gill filaments (Gosse, 1955; Fryer & Iles, 1972). Other entrapment structures, such as pharyngeal teeth and epibranchial organs, may participate in the retention of particles, although their functions are unclear. The presence of mucus, which participates in food consolidation and transportation, could improve the retention efficiency of the filter. In order to assess the contribution of the retention process in the feeding selectivity of planktivores (i.e., the retention efficiency), it is necessary to review the theoretical mechanisms by which biological filters remove particles from the water. For planktivorous fishes, the physical characteristics (speed and direction) of the water inhaled into the buccal cavity are very helpful in investigating the potential mechanisms of actual particle retention.

Mechanisms of particle retention by biological filters. Filtration is the process by which particles are removed from fluids, by the use of porous devices. But sieving is only one, among several, mechanisms involved. As industrial engineers use man-made filters, in which pores are several orders of magnitude larger than the particles trapped, to remove particulate matter from gases, Rubenstein & Koehl (1977) considered that, similarly, various mechanisms, in addition to sieving, could be responsible for the selectivity of biological filters. Characteristics of the suspended particles (such as size, shape, surface properties), the water flow (velocity, direction), and the filter (morphology, stickiness, physical or behavioural alteration capabilities of the mesh size, mode of particle transportation from the filter to the esophagus, ability to modify the cleaning rate of the filter) all have to be considered.

Beside sieving, direct or inertial interceptions of particles are mechanisms which can potentially be involved in the retention process of planktivores. Electrostatic attraction has not yet been demonstrated to be a determining factor. Gravitational and motile-particle depositions are probably insignificant mechanisms for fast swimming (i.e., tow-net filter-feeding) or sucking (i.e., pump filter-feeding and particulate-feeding) planktivores, but are important for suspension feeders filtering in slow currents (such as gorgonian corals, zoanthids, and others).

The probability of capture by direct (for small particles) or inertial interception (for large particles) is high when the particles adhere to the filter upon contact. Depending on surface properties of both the particles and the filter, 'sticky filters' (for example, covered by mucilage) can readily retain particles too small to be captured by sieving (i.e., smaller than the smallest mesh of the filter). Small organisms which possess elongated processes (such as filaments, spines, and others) are particularly vulnerable to interception by sticky filters. The retention efficiency of sticky filters is influenced by the density of small sized particles in the environment (which could be responsible for clogging the filter), the surface areas of the collecting structures which constitute the filter, and the water flow velocity. The prey morphology is obviously a determinant, as most of the prey organisms captured by planktivorous fishes are neither spherical nor regular in shape.

Zooplankters generally are non-spherical and have long antennae and legs covered by setae (such as copepods and euphausiids), diatoms form long-spined chains (for example, *Chaetoceros*), blue-green algae develop in long filaments (for example, *Anabaena* species), and Dinoflagellates have processes and protrusions (for example, *Ceratium* and *Peridinium*). These large elongated organisms, by increasing their surface areas (i.e., their gross size), are less susceptible to be ingested by, even large, filter-feeding zooplankters (but see the mechanism of gape narrowing between the edges of the carapace valves of large cladocerans in presence of dense net-phytoplankton: Gliwicz, 1980; Gliwicz & Siedlar, 1980), but become more vulnerable to retention on the branchial apparatus of filtering fishes, because of their appropriate size range. Filter-feeding fishes have increasing feeding selec-

tivities and rates for increasing sizes or chain lengths of phytoplankton. For example, menhaden's filtering rates increase with algal size (Durbin & Durbin, 1975; see Fig. 5A). 300–600 µm long trichomes (6 µm in diameter) of *Oscillatoria agardhii* together with *Aphanizomenon flos-aquae* dominate in the food of silver carp (Kajak *et al.*, 1977). As its gill racker spacings range from 20 to 25 µm (Voropaev, 1968), siver carp feeds selectively on particles larger than 20 µm (Boruckij, 1973).

Surface properties of the prey, which have been demonstrated to play an important role in the differential or selective feeding of small filter-feeding daphnids or copepods (Poulet & Marzot, 1978; Gerritsen & Porter, 1982), are probably less important in particle retention by filter-feeding fish. Because water moves, rather slowly, over (and not through) its filtering mesh, the particle retention of *Daphnia* is strongly influenced by the surface chemistry of the particles, which corresponds to their surface charge (ionic interactions) and wettability (hydrophobic-hydrophylic interactions) (Gerritsen & Porter, loc. cit.). The capture efficiencies for the smallest particles are greater for neutral than for net negatively charged particles, and decrease with increasing wettability (obtained by addition of a surfactant) of both the particles and the filter. Such a mechanism, which has not yet been demonstrated to occur in filter-feeding teleosts, probably may not contribute to the retention of the smallest particles by fish, because the water flow passing over the branchial apparatus is generally rapid, and thus the viscous forces are comparatively insignificant.

Although mucus covers the rakers of *Brevoortia tyrannus*, even prolonged experimental feeding trials on densities of small algae *Skeletonema costatum* higher than those found in coastal marine waters, never caused either a drop in the maximum particle size filtered (13–16 µm), or an increase of the feeding rate on the smallest particles with time, which both correspond to a clogging situation of the gill rakers (Durbin & Durbin, 1975). Consequently, these authors estimated that such a situation may be reached only in some extremely turbid estuaries with very high loads of detritus. But, it is conceivable that filter-feeding fish may alter their retention efficiency for a certain size range of prey organisms (the more abundant, or preferred, perhaps), by simply changing the rate at which they

clean their filters. For example, pump filter feeders may behave by slowing down their swallowing movement frequency. By doing this, accumulated particles, then functioning themselves as filters, could improve the retention efficiency for smaller particles. Another mechanism affecting the retention efficiency of the fish filtering apparatus has been suggested by Omarov & Lazareva (1974) for silver carp (*Hypophthalmichthys molitrix*): the fish could vary the quality and quantity of the mucus secreted under different food conditions.

Filtering efficiency. The gill raker spacings (also called gill raker gaps by King & McLeod (1976)) have long been considered as the most important determinant of the filtering capability in planktivorous fishes. King & McLeod (loc. cit.) proposed a formula for the computation of the gill raker gaps:

$$G = [T - (R \cdot W)]/[R - 1]$$

where T = the total gill arch length, R = the total number of rakers along the arch, and W = the mean raker width. However, the inaccuracy of this method when applied to three species of teleosts, made Nelson (1979) recommend direct measures of gill raker spacings rather than their computation.

Direct measurements of gill raker spacings may not be accurate in determining the lower threshold of filtration: they lead to a discrepancy between the expected size of the smaller prey retained by simple sieving through the filtering apparatus, and the size of the smaller prey effectively ingested (Kliewer, 1970; Seghers, 1975; King & McLeod, 1976; Durbin, 1979; Nelson, 1979), because either the considered fishes possess ramified gill rakers (microspines or denticles), or the surface properties of the gill rakers make them act as sticky filters. For the former type of fishes, denticle or spine spacings (when measurements can be done) rather than gill raker spacings may be better correlated with the size range of prey items ingested.

Comparing the diet and the morphological specializations of the branchial arches of three filter-feeding marine teleosts, Nelson (1979) observed that each species is capable of ingesting much smaller prey items than can be retained by its gillrakers by a simple sieve action. *Engraulis morfax* possesses rather fine gill raker gaps

(140–210 µm), while *Rastrelliger kanagurta* has finer denticle gaps (40–76 µm): when adult, the former is primarily zooplanktivorous, whereas the latter is predominantly phytoplanktivorous. Advanced structural specializations of the branchial basket occur among clupeids. An increased complexity of the gill rakers structure of *Brevoortia tyrannus* is associated with a change from a zooplankton to a phytoplankton diet during growth (June & Carlson, 1971). Radioisotope techniques demonstrate that juveniles of *B. tyrannus* (around 188 mm long) can filter phytoplanktonic cells (*Nannochloris*) ranging from 1 to 2 µm (Chipman, 1959; Peters, 1972), whereas the minimum size threshold for filtration (i.e., the smallest prey size at which the filtering rate differs significantly from zero) by adults is 13–16 µm (Durbin & Durbin, 1975). Similarly, the switching of *Ethmalosa fimbriata* towards dominant phytoplanktivory occurs with the development of an impressive three-dimensional system of ramified branchiospines on the edges of the gill rakers (Monod, 1949, 1961; Fagade & Olanyan, 1972). The filtering capability by simple sieving is thus extended down to 10 µm or smaller, while particle collection by inertial impaction probably increases by several orders of magnitude (Lazzaro, unpubl. data).

The functional morphology of the branchial basket of filter-feeding clupeids and scombrids reveals the importance of the denticle gaps in the collection of the smallest particles. The expansion of the branchial basket in a dorso-ventral plane provokes the erection of the gill rakers along the longitudinal axis of the branchial arch, and presents the denticle edges towards the direction of the water flow. Consequently, the denticle edges become the primary collection sites for the small particles, such as the solitary phytoplanktonic cells (Nelson, 1979). Nevertheless, complex raker structures (such as, for example, in *E. fimbriata*) make impossible the accurate assessment of the retention efficiencies for different particle sizes through direct measurements of denticle or raker gaps.

When direct measurements of the filtering gaps (i.e., the spacings between gill rakers, microbranchiospines, microdenticles) are possible, the filtering efficiency for a particular particle size can be calculated using the mean cumulative frequency of interraker distances (hyperbolic curve) as an estimate of the probability function for retention effi-

ciency (see modelisation procedures of retention efficiency by filter feeders in sections V.A.2. and V.A.3.).

The role of the epibranchial organs in the filter-feeding selectivity of fishes, as well as the mechanisms of food consolidation and transportation into the esophagus still remain unknown. Consolidation and transportation functions have been hypothesized for the epibranchial organs and the pharyngeal teeth, although their morphologies rather more suggest that they may play a role in the retention of prey items.

3. Particle digestion: resistance of phytoplankton to fish digestion processes

Since, at least, some filter feeders use phytoplankton as food, and some phytoplanktonic forms are resistant to digestive processes (such as, particularly, dinoflagellates and diatoms) it is essential to consider the fish digestion efficiency to assess the phytoplankton community responses to limnetic filter-feeding fish. Moreover, defecation of partially digested phytoplanktonic cells, immediately attacked by bacteria, contributes to the nutrient loading processes of lakes. In the elaboration of energetic models of grazing and predation by filter-feeding planktivores, the digestion event, in most cases, must be considered (see also the resistance of zooplankton to fish digestion processes in section III.A.5.).

Low gastric pH, associated with vigorous mechanical breakage in a gizzard-like stomach (often filled with fine sand grains), and prolonged exposure to digestive enzymes along a particularly long digestive tract are essential conditions for effective disruption of hard covered (i.e., the prokaryotic cell wall) phytoplanktonic cells, and the disintegration of their protoplasm (especially in colonial or filamentous blue-green algae *Microcystis* and *Anabaena*, diatoms, and dinoflagellates such as *Peridinium*). Digestive processes among Tilapias are extremely specialized to utilize more efficiently the algal resources. pH as low as 1.25 (Moriarty, 1973; Bowen, 1976; Caulton, 1976), and even 1.0 (Payne, 1978) can be reached by their stomach fluids during active digestion. Tilapias are particularly well adapted to destroy blue-green algal cell walls (Bowen, 1982), but not all fishes are so efficient.

The presence of numerous viable algal cells in the feces of herbivorous planktivores is not rare among various groups of fishes. For example, in Cichlidae: Spataru & Zorn (1978) observed that *Microcystis* spp., and frequently *Peridinium* spp. had their integrity after passage through the gut of *T. aurea*. Preliminary experimental cultures of fecal pellets freshly released by *T. aurea* fed twice a day, exclusively on natural lake plankton, led within a few days to a rapid algal growth (Lazzaro, pers. observ.). But, *Peridinium cinctum*, the preferred food of *S. galilaeus* in Lake Kinneret (Israel), had broken-up theca and progressively more digested protoplasm, down to the end of the fish digestive tract (Spataru & Zorn, 1976; Gophen, 1980; Drenner *et al.*, 1982c). In Cyprinidae: Malyarevskaya *et al.* (1972), using epifluorescence microscopy, detected great amounts of dead and live cells in the excrements of herbivorous silver carp, fed on toxic blue-green algae *Microcystic aeruginosa*. No differences were observed by Kajak *et al.* (1977) between the structures of filamentous blue-green algae cells (mainly colonial forms of *Aphanizomenon flos-aquae*, selectively ingested) in the final part of the gut of silver carp, *Hypophthalmichthys molitrix*, and in the plankton of four Masurian Lakes (North-Eastern Poland), demonstrating that these algae were not digested. Moreover, in periods of mass 'water-blooms' of filamentous blue-green algae, fish kept in net cages suffered high mortality rate, due to their lack of access to bottom food sources, and smaller size range of algae. Unlike the blue-greens, *Ceratium hirundinella* and diatoms were well digested, as crushed sculptured envelopes of *C. hirundinella* and empty diatom frustules were abundant in the final part of the fish gut. According to Prowse (1964), most phytophagous fishes digest only diatoms, but do not digest Chlorococcales, Eugleninae, and blue-green algae. Savina (1965) showed that *Oscillatoria granulata* Gardner and *Anabaena wernerii* Brunnth, passed undamaged through the guts of silver carp, whereas only diatoms and Protococcales were digested. In addition, Vovk (1974) demonstrated that decomposing algae were better assimilated than live ones. In Clupeidae: Velasquez (1939) and Smith (1963) found 46 genera of algae (mainly Chlorophyceae and Myxophyceae) which survived gizzard shad gut passage.

IV. Evaluation of selective feeding: a review of electivity indices, their strengths and limitations

To quantify selective predation, different measures of preference are used (see reviews in Chesson, 1978, and Lechowicz, 1982; see also Fig. 7) based on the comparison between measurements of the relative occurrence frequencies of prey types (or prey species) in a predator's diet and in its environment.

First, some caution must be used in the interpretation of the predator's stomach contents. The main problem is our own estimation of prey 'availability' in the environment, which depends principally on the sampling device used (see a review of limitations in O'Brien & Vinyard, 1974). One question the fish feeding ecologist is interested in answering is: 'which prey items present in the predator's environment are really "available" to this predator?' It may be answered by examining whether the prey is consumed (a lot or not much), or not. The availability of one prey item to a particular predator is a result of the relative physiological and behavioural properties of both the predator and the prey. Werner & Hall (1974) and Mittelbach (1981) used laboratory experiments to estimate availability. Prey consumption is affected by prey size, shape, pigmentation, contrast, motion behaviour and escape ability, while predator efficiency is affected by its sight, preference, experience, hunger, feeding behaviour, and capture success.

It is obvious that the detection and capture abilities of a fish for one particular prey are dependent upon the conspicuity and escape behaviour of this prey, while the sampling of this same prey by the experimenter is only dependent upon the selectivity of the device used. Thus, one prey abundantly captured in the environment by the experimenter might be absent from the stomach contents of the fish, only because it cannot be seen or captured by the fish. Moreover, to measure electivity, one needs to know the horizontal and the vertical distributions of both fish and prey during the feeding period preceding the fish capture (O'Brien & Vinyard, 1974).

An additional bias can result from differential prey digestion rates which may affect measures of selectivity based on stomach content analysis. Since quickly digested prey tend to be underestimated in the fish diet, they may be considered as

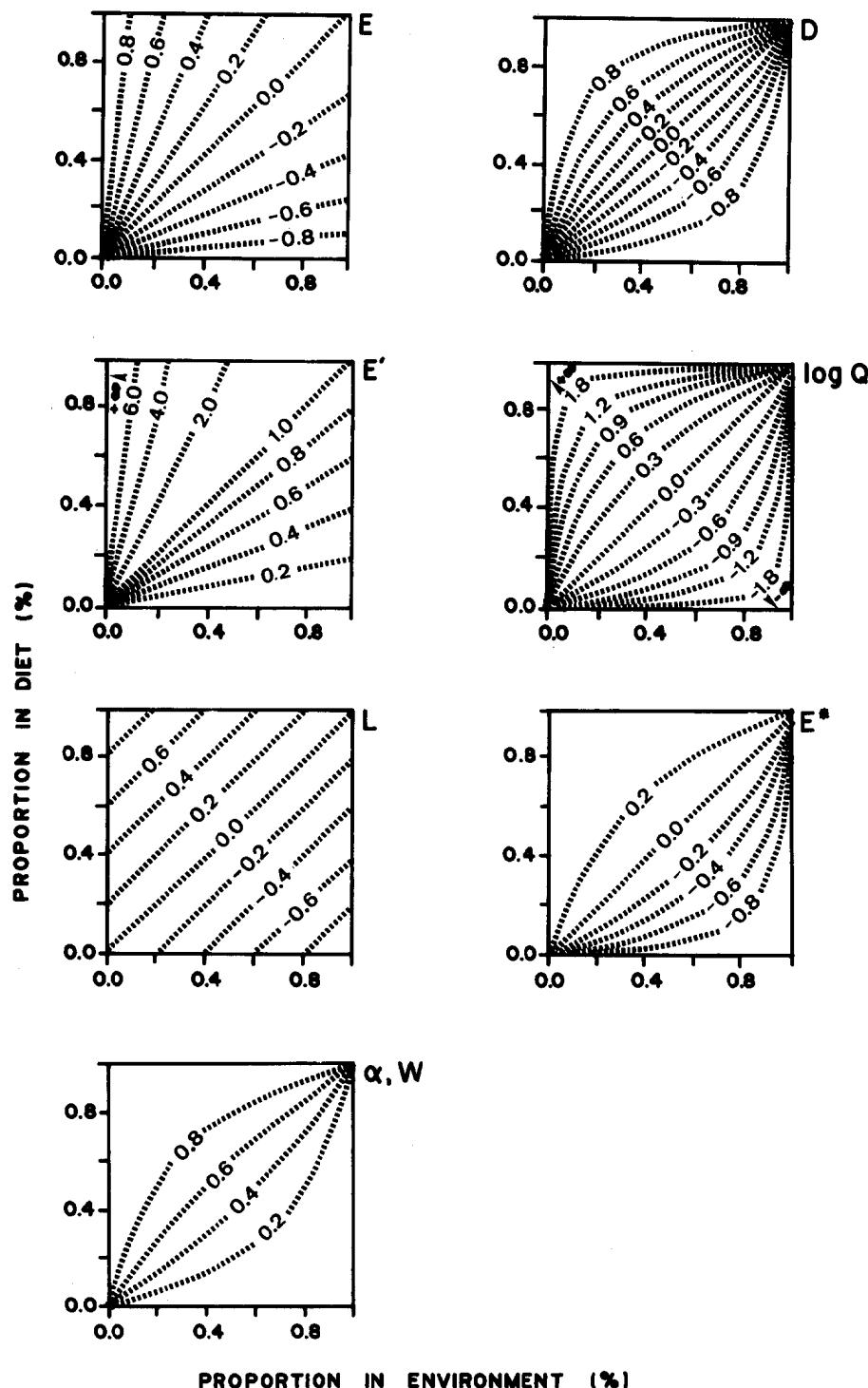


Fig. 7. The values of various electivity indices as functions of availability (π_i) and utilization (r_i) of a food item i : Ivlev's electivity index (E); forage ratio (E'); Jacob's modified forage ratio ($\log Q$); Strauss' linear preference index (L); Chesson's and Vanderploeg & Scavia's relativized forage ratio (α, W); Vanderploeg & Scavia's relativized electivity index (E*) (from Lechowicz, 1982).

apparently negatively selected (i.e., avoided) although this may be false (Gannon, 1976). This situation occurs in alewife (Rhodes, 1971), where *Daphnia* the most rapidly digested of any zooplankter tested (including *Mesocyclops*, *Cyclops*, *Bosmina*, *Simocephalus*, and midge larvae *Chironomus*) in fish stomachs, appeared to be avoided when measures of selectivity were applied. Similarly, *Daphnia* was verified to have higher passage rate from the stomach of bluegill sunfish (Werner *et al.*, 1981), and *Daphnia* plus other small food particles to pass through fish stomach faster than larger items (Windell, 1978).

The most simple indice, initially proposed by Shorygin, is the forage ratio indice (FRI) of Edmonson & Winberg (1971):

$$FRI = ri/pi$$

where ri = the ration of food type i , and pi = its proportion in the environment. FRI values range from 0 (avoidance) to $+\infty$ (when selection is highly positive). FRI = 1 for random eating, i.e. no selection or avoidance occurring: the prey type i is consumed in the same proportion as it is present in the environment.

The most commonly used measure of electivity is the indice Ei of Ivlev (1961). Its calculation is a simple ratio:

$$Ei = [ri - pi]/[ri + pi]$$

where ri = the proportion of food type i in the fish's ration, and pi = the proportion of the food type i in the environment. Ei values range from -1 (avoidance) to +1 (positive selection). When $Ei = 0$ there is no selection: the food is eaten in the same proportion as it is present in the environment. Ei values between -0.3 and +0.3 are generally considered not significantly different from 0, and thus to indicate non-selective feeding.

These two indices present a main weakness: both are highly influenced by the relative abundance of the prey types in the environment. For example, given a fixed proportion of the food i in the predator's diet ($ri = \text{constant}$), an increase of the abundance of i in the environment (pi) decreases the predator electivity for this food, whereas its preference for this food remains unchanged.

Modified versions Qi and Di of FRI and Ei were

proposed by Jacobs (1974) in an attempt to achieve independence from the influence of the relative abundances of the prey types in the environment. In fact, Di is only slightly less sensitive to sampling errors for rare prey types than either Ei or FRI, while Qi is unusually sensitive when either ri or pi is less than about 0.1 (Lechowicz, 1982). They are defined by:

$$\begin{aligned} Qi &= [ri(1-pi)]/[pi(1-ri)] \\ Di &= [ri - pi]/[ri + pi - 2ripi] \end{aligned} \quad \text{and}$$

where ri and pi have the same definitions as those above.

Jacobs recommended the use of $\log Qi$ and Di in laboratory feeding trials as differential mortality rates, to quantify the selection of food i relative to food j . i and j may be two specific food types or groups of food types. j may be also the sum of all food types in the environment, except food type i .

Quotient Qi varies from 0 to +1 for negative selection, and from +1 to $+\infty$ for positive selection. Relative difference Di varies from -1 to 0 for negative selection and from 0 to +1 for positive selection. With the range of $\log Qi$ from -0.6 to +0.6, there is no 'a priori' difference between $\log Qi$ and Di measures.

In order to overcome the problem of variation of selectivity measure variation with the abundance in the environment of the foods other than the considered food i , Chesson (1978) proposed a measure of preference (α_i) based on a simple biological stochastic model involving probability of encounter and probability of capture upon encounter. Chesson provided a normalization of Ivlev's forage ratio defined by:

$$\alpha_i = [(1 + Ei)/(1 - Ei)] / [\sum_{i=1}^m (1 + Ei)/(1 - Ei)]$$

Here, m = the number of prey types, and Ei = the measure of electivity (Ivlev's indice) calculated for prey type i , with $\sum_{i=1}^m \alpha_i = 1$.

When $\alpha_i = 1/m$ (with $i = 1, \dots, m$) selective predation does not occur, when $\alpha_i > 1/m$ more of species i occurs in the diet than expected by random feeding, and when $\alpha_i < 1/m$ less occur than expected.

Preference $\alpha = [\alpha_1, \dots, \alpha_m]$ reflects any deviation from random sampling of the prey in the environment. Alternatively, α can be derived from

the proposed stochastic model of prey encounter and capture which accounts for: prey distribution, prey visibility, searching behaviour of the predator, pursuit upon encounter, escape ability of the prey, capture efficiency of the predator, preference for prey, experience, hunger, time and predation constraints for feeding. Based on a biological model, α_i is a useful measure for quantifying predator preference.

Paloheimo (1979) assumed that a preference indice really independent of relative prey abundances can be derived from standardized forage ratios, so that the sum of the forage ratios of the different prey types equals one. So, he recommended a normalization of FRI which can be defined by:

$$NFRi = [ri/pi] / [\sum_{i=1}^m ri/pi]$$

Vanderploeg & Scavia (1979) proposed the same expression symbolized by Wi . It is convenient to note that although α_i , Wi , and $NFRi$ are presented as different, in fact they are identical, since:

$$[1+Ei]/[1-Ei] = [1+(ri-pi)/(ri+pi)]/[1-(ri-pi)/(ri+pi)] = ri/pi$$

and similarly $\sum_{i=1}^m [1+Ei]/[1-Ei] = \sum_{i=1}^m ri/pi$

$$\text{then } \alpha_i = [ri/pi]/[\sum_{i=1}^m ri/pi] = Wi = NFRi$$

Thus, α_i , Wi , and $NFRi$ have the advantage of being independent of the relative abundance of food types, and are therefore appropriate for meaningful comparisons between samples having the same number of food types. But, they have the undesirable property of being sensitive to the duration of the feeding experiment (Pearre, 1982). In that way, they are similar to Ei which is also affected by experimental duration and depends on the initial spectrum of prey distributions (Vanderploeg & Scavia, 1979).

To avoid some undesirable properties of either Ei or FRI , such as dependence upon relative and absolute sample sizes and relative abundance and rarity of prey species in the environment, and to permit statistical comparisons between samples, Strauss (1979) proposed a simple linear indice:

$$Li = ri - pi$$

which ranges from -1 (avoidance or inaccessibility)

to $+1$ (preference). The indice value for random feeding is 0 under all conditions. The normal distribution of Li allows statistical comparisons between calculated values, or between a calculated value and a null hypothesis value (such as 0).

But, Li suffers the identical disadvantages that Ivlev's and Jacobs' indices do: (1) Li is vulnerable to sampling error for prey rare in the environment or in the diet (and particularly more vulnerable as pi increases), and (2) extreme indice values only can be reached under unrealistic conditions where $ri = 0$ and $pi = 1$ ($Li = -1$), and $ri = 1$ and $pi = 0$ ($Li = +1$). Unfortunately, with Li it is not possible to compare electivities for a particular prey item between samples where the abundances of prey items are different, either in the environment, or in the diet. This main weakness eliminates any comparison between electivity values obtained from the field.

Moreover, its main disadvantage is that preference rankings obtained from Li measured on field data disagree with rankings by other indices (Lechowicz, 1982).

To achieve a possible range from $+1$ to -1 and 0 value for random feeding, Vanderploeg & Scavia (1979) proposed a relativized electivity indice Ei^* similar to Ivlev's Ei , but using the selectivity coefficient Wi and the number m of food types available in the environment:

$$Ei^* = [Wi - (1/m)] / [Wi + (1/m)]$$

Similar to α_i , Ei^* is a measure of preference which estimates any deviation from random feeding and makes possible comparisons of electivity rank orders between samples. Nevertheless, some undesirable properties still remain: (1) as for Li , the maximum preference value ($Ei^* = 1$) can only be reached under unrealistic conditions where $ri = 1.0$, $pi = 0.0$, and $m = \infty$, (2) when m increases, Ei^* becomes more vulnerable to sampling errors for food rare in the diet or rare to moderately common in the environment, and (3) parametric statistical comparisons of electivities are only amenable between samples with the same number of food types.

Electivity indices give general information on the quantitative feeding patterns of predator. But, often, observed feeding preferences need to be statistically tested to know if the predator feeds at random on available prey types, if respective preferences differ between samples, or if two prey types

are really preferred in a differential manner under certain conditions.

Thus, to provide appropriate means for significance testing, Pearre (1982) proposed two statistically testable indices derived from a chi-square formulation with one degree of freedom:

$$Vi = [niNo - noNi]/[abde]^{1/2}$$

$$\text{and } Ci = \pm [|niNo - noNi| - n/2]^2/abde]^{1/2}$$

where the sign of Ci is given by the consideration of ($niNo - noNi$), Ni and No are respectively the number of any prey type i, and the sum of all other prey types except i in the environment, ni and no are respectively the corresponding numbers in the diet, and $a = ni + Ni$, $b = no + No$, $d = ni + no$, $e = Ni + No$, and $n = ni + Ni + no + No$.

Because neither α_i nor W_i can be directly tested, the calculation of Vi and Ci may be a good measure of selection probability of any sample size.

Finally, Gras & Saint-Jean (1982), wishing to relate the stock of planktivores to the stock of plankton useful for planktivores through prey selection considerations, proposed a normalized-like forage ratio Si, defined by:

$$Si = [ri/pi]/[rR/pR]$$

where R is a reference prey which must satisfy several conditions, of which the first important is to be one of the most selected prey (i.e., which has the highest FRI value). The selection indice Si is expressed as the ratio FRI/FRR, with SR = 1 and $Si < 1$ for $i = R$. Thus, Si represents the percentage of selection of prey i in comparison to prey R.

These authors used Si to assess the useful biomass of prey $Bu = \sum_{i=1}^m SiBi$, where Bi is the biomass of prey i, and Ce = Bu/Bt the collecting efficiency of the predator (i.e., the useful fraction of prey biomass), where Bt is the total biomass of prey.

A hindrance decision has to be made on the choice of the reference prey R, since several prey types may be taken as reference prey, and prey R is frequently different between samples. To make rR/pR as accurate as possible by minimizing sampling errors, the reference prey R must not be only easily identified, and abundant both in the environment and in the diet, but particularly, must be the most highly positively selected prey.

Gras & Saint-Jean (loc. cit.), investigating the decrease in the stock of the filtering planktivore *Brachysynodontis batensoda* (Mochokidae) in Lake Chad during the lowering of the water level, concluded that a decrease in the useful fraction of the zooplankton biomass (Bu/Bt) may well play a role in the growth slowing down of the planktivore. To show that, they used the large, spherical, slow moving cladoceran *Moina micrura* as reference prey.

They proposed another way to calculate Si, without calculating α_i and p_i , for various sample series having the same reference prey. In this particular case, Si can be expressed as:

$$Si = [N'i/Ni]/[N'R/NR]$$

where Ni and NR are, respectively, the density of prey type i and the density of the reference prey R in the environment, and N'i and N'R are the numbers of the same prey types in the diet. The expression of Si possesses the important property of being effectively independent of the relative abundances of prey types, because it is based on absolute prey densities.

But, Si presents two main weaknesses: (1) the collecting efficiency of the reference prey (SR) is unrealistically assumed to be equal to 100%, and (2) the measures of collecting efficiencies in a sample depend closely on the choice of the reference prey.

As emphasized by Paloheimo (loc. cit.), the indices FRI and Ei on the one hand, and Qi and Di on the other hand, are directly deductible one from another:

$$Ei = [FRI - 1]/[FRI + 1], \quad \text{and} \\ Di = [Qi - 1]/[Qi + 1],$$

and the necessity to have two indices is not justified. Similarly, as previously demonstrated: $\alpha_i = Wi = NFRi$.

Nevertheless, the main conclusion which can be drawn from the critical analyses following the works of Ivlev is that no indice based on prey countings in the diet and in the environment can furnish an absolute predator feeding preference, except in the extreme case (rather rare) where a predator consumes one or two prey types among many available prey types. This conclusion, implicit in some works (Gras & Saint-Jean, loc. cit.; Lechowicz, loc. cit.), is clearly demonstrated by

Paloheimo (loc. cit.). At best, these indices represent the 'apparent selectivity' for different prey types, according to changeable modalities (often unknown), such as combination of 'sensu-stricto' preferences, capture capabilities, respective distributions of predator and prey, and so on.

In correct terms, it turns out that: (1) the minimum of information which can be expected from an electivity indice is a prey ranking by increasing (or decreasing) order of apparent selection, and (2) the maximum of information is the expression, by proportional factors, of differential selections between prey (for example: the prey ranked first with an indice value of x is two times less selected than the prey ranked second with an indice value of $2x$).

From the comparative analyses conducted by Paloheimo (loc. cit.), Gras & Saint-Jean (loc. cit.), Lechowicz (loc. cit.), and Pearre (loc. cit.), it can be concluded that: (1) all indices provide similar rankings of food preferences, except Strauss' Li which gives changeable rankings according to the relative abundances of prey in the diet or in the environment, (2) the indices Ei, Qi, Di (and Li) vary with relative abundances of prey, and obscure or modify variably the proportional factors which express the differences in selection between prey (it could be demonstrated that Ei* follows this general trend (Saint-Jean, pers. commun.); in this sense, the respective behaviours of Vi and Ci might be profitably tested), and (3) only the indices FRi, NFRi (thus α_i and W_i), and Si give the maximum of information. See also Fig. 7.

Among the last three indices, FRi must be excluded because its absolute value varies with the abundance of prey, which makes comparative studies difficult. This variation factor is eliminated from NFRi and Si, which therefore have the double advantage of being independent from the relative abundance of prey, and to reflect accurately the differences in apparent selection existing between them.

NFRi has the advantage over Si of not requiring any preconditions, and representing a single, identical, measure of selection, applicable to any situation. Nevertheless, its main weakness is to vary with the considered number of prey. Si expresses more directly (directly if $1/Si$ is utilized) the previously mentioned proportional factor showing the differential selection between prey. As already mentioned, Si may be used to assess the fraction (B_u) of the prey stock available to a predator, based on

its selective foraging pattern. 'A priori', this data could permit close quantitative analysis of the relationships between plankton and planktivores.

Another potential advantage of Si is that it could be calibrated, by comparing experimentally the selectivity for the reference prey with the selectivity for a standard prey which might be, for example, a spherical inert particle having a well known diameter and a maximum collecting efficiency. A similar approach as been used by Drenner (1977) to assess capture efficiencies of a siphon-like pump filter-feeding planktivore for different prey types, using air bubbles and heat-killed zooplankton as standard prey having maximum capture probabilities.

In fact, Si possesses other potential uses, which emphasize the importance of this kind of indice: its significance remains to be explored. 'A priori', the problems might arise with the choice of the reference prey (or group of prey), and with the variability of the intrinsic selective feeding pattern of the predator. Apart from these problems, the weakness of Si is that, expressed as a ratio based on particular prey (i.e., the reference prey), it cannot represent a general measure of selection. As previously mentioned, only NFRi can fit this criterium.

It follows firstly, that the complementary use of these two indices could be recommended, which otherwise are simply related:

$$Si = NFRi/NFRR$$

The main conclusion which can be reached from the critical analysis of the use of these electivity indices is that they are only 'relative measures of preference'. In the present review paper, I follow the conventional and most commonly used terms concerning relative food selection: i.e., avoidance (or negative preference), random feeding, and (low, medium, highly positive) preference.

Since these measure of relative preference reflect not only the predator 'preference' (behavioural and/or mechanical), but also the relative prey abundance, the prey detectability, and the prey capture ability, the indices of electivity are composite. Thus, they are useful for discerning and comparing feeding patterns, but obviously not meaningful for predicting levels of food utilization. The latters can only be done through the use of appropriate measures of food intake, like the various available expressions of feeding, filtering, and ingestion rates.

V. Models of prey selection

A. Model conceptualization and feeding modes

Within the last 20 years, there have been several very interesting theoretical works on the area of prey selection by planktivorous fishes. A large body of theory has been developed to explore and predict how foraging patterns of planktivorous fish are related to plankton composition and density. A considerable attention has been paid to optimal foraging theory, but relatively few field tests of optimal foraging models have been attempted (e.g., Werner *et al.*, 1983a, 1983b). A predictive theory of individual fish foraging pattern has been used as a mechanistic basis of a more comprehensive theory on the selective utilization of plankton species by planktivore populations. Most models of prey selection were dedicated to particulate feeders, and especially to the mechanisms by which fish concentrate feeding on particular zooplankton size classes upon detection. Few models have concerned filter feeders, probably because most research have been done in temperate zones where visual planktivores are generally dominant.

In natural or man-made aquatic ecosystems, predation models are useful tools to assess and predict qualitative and quantitative utilization of planktonic resources, and shifts in plankton composition and abundance in relation to changes in the nature and/or the predation level of planktivores. They accurately help decision making in the field of lake or reservoir management in order to (1) preserve adequate water quality levels for drinking or recreational uses, and/or (2) optimize planktivore production for sport fishing (where planktivores are used as fish foods for piscivores), craft or commercial fisheries.

Theories related to mechanisms of diet optimization (such as, for example, energy maximization per unit of time) have been abundantly used to build models of predation by planktivorous fishes. Nevertheless, Zaret (1980) emphasized that sensory cues (such as, vision, chemoreception, and mechanoreception), hunger, experience, and feeding repertory, rather than actual energetic considerations (realistically unmanageable by a fish), are factors which can readily govern the foraging pattern and the feeding selectivity of planktivores. Factors such as hunger and learning are easily in-

corporable into an optimization framework, as they are simply constraints that, if added to foraging models, modify the predictions of prey selection (Werner, in litt.).

The original approach used by Holling (1966) to examine the predation-act has been followed in numerous studies dealing with the feeding selectivity of planktivorous fishes (among which those of Ware, 1973; Werner & Hall, 1974; O'Brien *et al.*, 1976; Drenner, 1977; Eggers, 1977; Durbin, 1979; O'Brien, 1979; Gibson, 1980; Wright & O'Brien, 1984). The approaches used have been proposed as quantitative models able to predict the potential impact induced by changes in the level of predation pressure from particulate feeders, or pump filter feeders, on the structure of the zooplankton communities. The vulnerability of a prey type *i* to a particular planktivore can be estimated by its probability of being consumed by the fish. This probability is the product of the conditional probabilities that each event constituting the predation-act is successfully completed (O'Brien, 1979; Wright & O'Brien, 1984; after Holling, 1966). The vulnerability (*Vi*) of a prey type *i* to the consumption by the planktivore (i.e., the efficiency of the fish to consume that prey type) is a function of both its ingestion and digestion probabilities (noted *Ii* and *Di*, respectively):

$$Vi = Ii \cdot Di$$

Since the sequence of successive events which determines the probability of ingestion is dependent upon the feeding behaviour used by the fish, distinct expressions are proposed for particulate feeders, tow-net filter feeders, and pump filter feeders (see below in the respective sections). Because these functional relationships can be measured experimentally, they may help to discern the relative importance of various mechanisms responsible for differential patterns (selective or not) of prey collection and consequent dietary prey distribution. Potentialities of feeding selectivity can be investigated for a fish using the appropriate expression (according to the knowledge of the feeding repertoire the fish can display at particular sizes (i.e., ages), and to the physical characteristics of the aquatic environment) applied to the entire set of (readily) available prey types. These last can be identified from the knowledge of the respective migratory behaviours of the fish and the prey which determine

the duration of exposure of the prey to fish predation pressures, and the relevant prey characteristics for detection, pursuit (these two for particulate feeders only), capture, retention, and digestion.

Below, in the first part of this section, and for each planktivore feeding mode, the main models available are discussed, and then, following the Holling's approach of the predation-act, equations for differential prey vulnerabilities and differential feeding rates on prey are presented. In the second part of this section, the need to consider eventual switches of feeding modes in response to (seasonal) changes in resources within an habitat, or to (spatial) differences between habitats successively explored, are emphasized to improve the flexibility and the realism of the modelling approach.

1. Particulate feeders

Quantitative models, most of them based on optimal foraging theories, have been used to attempt the description of the modes of prey selection and the feeding strategies of visual planktivorous fishes (Werner & Hall, 1974; Confer & Blades, 1975; O'Brien *et al.*, 1976; Eggers, 1977; Gerritsen & Strickler, 1977; Gibson, 1980; Gardner, 1981; Eggers, 1982; Wright & O'Brien, 1984; see reviews on optimal foraging approaches in Mac Arthur & Pianka, 1966; Schoener, 1969, 1971; Werner, 1972; Krebs, 1973, 1978; Charnov, 1973, 1976; Pearson, 1974; Pyke *et al.*, 1977; Pyke, 1979; Charnov & Orians, 1979; Mittelbach, 1981; Werner *et al.*, 1983a, 1983b).

One of the first models using an optimization approach based on time constraint for feeding activities was proposed by Werner & Hall (1974). This 'optimal foraging model', based on differential visibility of prey, maximizes the net energy intake per unit of time for each prey eaten by bluegill sunfish in experimental ponds. The conceptualization of this model is developed in Werner (1972). At low densities of different-sized instars of the cladoceran *Daphnia magna*, bluegill are not selective and prey items of different sizes are eaten as detected. With increasing prey densities, however, fish select the largest prey sizes, while the smaller sizes are ignored. As the prey densities increase, prey sizes are eliminated from the diet sequentially, beginning with the smaller ones. As in accordance with Ivlev's (1961) observations, at higher prey densities the

breadth of the fish's diet decreases and the fish becomes more selective on the basis of prey size. This is consistent with the more recent studies of Eggers (1977) and Miller (1979). Werner & Hall (*loc. cit.*) attributed this change in diet breadth to the ability of fish to respond to prey density changes in an 'optimal foraging' pattern (based on cost of prey capture in terms of energy and time), although they did not describe its mechanism. Their model is more adapted for high prey densities, when the swimming distance of fish is larger than the reactive distance of prey (i.e., the distance at which a prey is detected; see section III.A.1.) or when several prey are often detected simultaneously. It assumes that a prey detection probability is proportional to the cube of its reactive distance.

A model more appropriate for low prey densities, when the swimming distance is larger than the reactive distance, was developed by Confer & Blades (1975) for *Lepomis gibbosus*. They proposed that the detection probability is rather proportional to the square of the reactive distance, because when moving from prey to prey the fish search out cylindrical volumes. Calculating values of Ivlev's (1961) electivity index, they showed that Galbraith's (1967) data and the measurements of fish reactive distance reported in Werner & Hall (*loc. cit.*) and in their own work support a model of continuous increase in fish predation intensity with prey size. They demonstrated that reactive distance is a linear function of prey size. But, differential prey conspicuity (size, plus motion behaviour) and escape ability may affect reactive distances of similar-sized prey. More translucent *D. pulex* elicit significant shorter reactive distances than similar-sized *D. magna*. *Mesocyclops edax*, a vigorously swimming copepod, elicit longer reactive distances than similar-sized *Diaptomus sicilis* copepodites and adults. The regression line for copepods is steeper, with a lower intercept, than that of cladocerans (even *Daphnia*). Small copepods elicit significantly smaller reactive distances than either *Daphnia* of the same size. The reactive distance of the largest 2.3 mm *Diaptomus leptopus* females is not significantly different from that of a 2.3 mm *D. magna*. Some copepod species are highly successful at eluding capture: the capture ability of *D. sicilis* by *L. gibbosus* is 21% compared to 61% for *D. ashlandi*. This conflicts with the model of Allan (1974) who proposed that the intensity of fish predation on

cladocerans increases with prey size up to some intermediate size after which predation intensity remains constant. Looking at the energy ingestion by *L. gibbosus* in presence and absence of predaceous zooplanktonic prey (*D. sicilis*, *Epischura lacustris*), Confer & Blades' model predicts that, large and more conspicuous, predaceous zooplankton increase the energy uptake of planktivorous fish.

Based on the predation cycle, Eggers (1977) used a 'differential detection rates model' to analyse the effects of prey distribution, detection rate, handling time, capture success, and optimal foraging on zooplankton selection by visual planktivores. He established that the prey detection rate is the product of the reactive field volume by the prey density. Since the visibility of a prey underwater depends upon its contrast with the background, the limits of the fish visual acuity are given by the contrast threshold above which prey are detected. The contrast threshold is not constant but decreases with increasing area of the retinal image, and increasing water illumination to which eyes are acclimated. The apparent contrast of a prey underwater can be expressed as:

$$Ca = Co \exp(-\alpha D)$$

where α = the water extinction coefficient, and D = the distance between the prey and the retina. Co is the inherent contrast of the prey defined by:

$$Co = (Ib - Io)/Ib$$

where Ib = the illumination of the background (expressed in light flux per unit area) and Io = the illumination of the prey. As defined, Co is independent on prey size or shape. However, differences in colors among prey are responsible for differences in inherent contrast. The area of the retinal image (RA) depends on the surface area of the prey projected (PS) onto a plane perpendicular to the sight line and the distance (D) between the retina and the prey:

$$RA = f PS/D^2$$

where f = the focal length of the eye.

To compute the maximum reactive distance, three situations must be distinguished. First, when the inherent contrast of the prey is high, the maxi-

mum reactive distance, which is proportional to the square root of the projected surface area, increases with prey size. For similar-shaped prey, the reactive distance is proportional to the prey length. But, rounded prey which have a greater projected surface area, are detected at a greater distance than elongated prey of similar size. This is consistent with Confer & Blades' (loc. cit.) observation, where individual *Daphnia* (round body) have greater reactive distances than similar-sized individual copepods (long body). Mobility increases the retinal area stimulated. Thus, moving prey are detected at greater distances than non-moving prey. Second, when the inherent contrast of the prey is low, turbidity is high, or light intensity is low, reactive distances are independent of prey size or shape. Third, when the water illumination to which fish eyes are acclimated decreases, the contrast threshold decreases. The resulting effect on reactive distance is obscured by interactions between water illumination, contrast threshold, extinction properties of the water, and area of the retinal image.

Because fish are very large and mobile compared to their prey, handling times (i.e., time needed to pursue, capture, retain, and digest prey) are short, and differences among prey types are likely to be negligible. Handling time per prey is also assumed to be constant in Werner & Hall's model. The handling time is inversely related to hunger (Ware, 1972), and increases exponentially as prey size reach the planktivore mouth gape (Werner, 1974).

Some zooplankter forms are able to avoid capture by darting out of the fish visual field. The capture efficiency (i.e., the proportion of prey pursued that is successfully captured) increases with fish size (i.e., age), and is specific to prey type.

For a particular prey assemblage, the strategy of prey selection that maximizes the energy intake rate is unique (Mac Arthur & Pianka, 1966; Werner, 1972; Charnov, 1973, 1976; Pearson, 1974; Werner & Hall, 1974). The optimal set of prey consists of all prey whose expected energy intake per handling time is greater than a given value. It is derived by mathematical analysis performed on a prey distribution ranked according to the ratio of energy intake to handling time. Werner (1972) and Werner & Hall (1974) implied that this ratio increases with prey length. But, this may not be valid if larger individuals of a given prey type escape better the fish capture. In such a case, the fish may avoid pursuing

larger and more evasive individuals of a prey type, in order to maximize energy intake. Eggers (loc. cit.) emphasized that the assumed optimization criterion for foraging time may be incorrect, as the fish must be able to discriminate between prey types according to the assumed criterion, or, at least, to some highly correlated factor (Schoener, 1971). For two limiting cases, Schoener (loc. cit.) demonstrated that, to maximize the net energy intake rate while foraging, the optimal foraging strategy was to minimize foraging time when the predator was constrained by minimum energy requirement, or to maximize energy assimilated when time available for foraging was limited.

The 'apparent-size model' of prey selection described for bluegill sunfish (O'Brien *et al.*, 1976; Vinyard, 1980), and white crappie, *Pomoxis anularis* (Wright & O'Brien, 1984), assumes that the predator choice between prey is based on the prey's apparent sizes (see Fig. 8). The apparent size of a prey is defined as its angular height subtended at the fish's eye. When two prey, differing in apparent size by an arc tangent of, at least, 0.2 degree (0.4 degree for white crappie) are offered, bluegill sunfish

selects the apparent largest prey. However, when *Daphnia* and *Diaptomus* are offered at the same time, the pursuit probability is higher for *Daphnia* than for *Diaptomus* of equal apparent size (Vinyard, loc. cit.). Vinyard demonstrated also that when one *Daphnia* and one *Diaptomus* are offered simultaneously, the average percentage of choice for the non-evading prey (*Daphnia*) increases with the increasing number of feeding trials and reaches a maximum value of about 90–95%. These results suggest a substantial intrinsic preference of bluegill for *Daphnia* which might be attributed to some learning process. An alternative interpretation (Confer & Blades, 1975; Eggers, 1977) could be that the round body of *Daphnia* stimulates a greater retinal image area than the elongated body of similar-sized *Diaptomus*. Nevertheless, in the same situation, *Diaptomus* is selected in favor of *Daphnia* by *Perca fluviatilis* (Furnass, 1979). According to Wright & O'Brien (loc. cit.) this inverse preference could only occur when *Diaptomus* is not moving. Thus, interspecific pursuit choices would be based on the comparison of differential specific motion behaviours of the prey. Nevertheless, the basic assumption of the 'apparent-size model' conflicts with the fact that the size of the retinal image of a prey object is determined by its area rather than by the visual angle subtended (Lamar *et al.*, 1947).

Gibson (1980) tested the apparent-size model for three-spined stickleback (*Gasterosteus aculeatus*) over a wide range of densities of two size classes of *D. magna*, and found that the model was valid below visual densities of 1100 prey per visual field, and failed above. He emphasized that an alternative mechanism of prey choice must be operating under high prey densities. As many recent works are demonstrating that fish can discriminate between different-sized prey (see Werner *et al.*, 1983b), Werner (in litt.) believes that fish do not always use apparent-size in prey selection. Comparing the optimal foraging model with alternative models of differential detection rates and apparent-size, Werner *et al.* (1983b) showed that bluegill actively selects zooplankton according to prey sizes and densities, as well as to the energetical cost of procuring them. Werner *et al.* (loc. cit.) agreed with Kramer (1979), Mittelbach (1981), and Eggers (1982) that bluegill do not appear to feed by apparent-size.

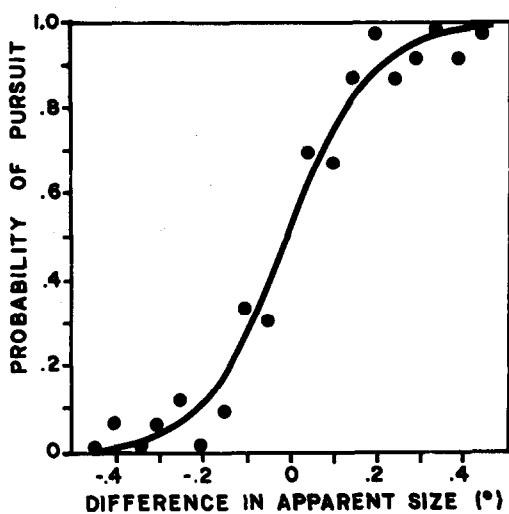


Fig. 8. Apparent size choices for white crappie (*Pomoxis anularis*, Centrarchidae) simultaneously presented two *Daphnia magna*. Each point designates a 0.05 angle interval. The right-hand side of the graph represents the percentage of the time the apparently larger prey is initially pursued. The left-hand side represents the percentage of the time the apparently smaller prey is initially pursued. The curve is fitted by eye (from Wright & O'Brien, 1984).

As mechanisms involved in size selective predation at high prey density (i.e., several zooplankton detected simultaneously) remained unclear, Gardner (1981) tested the differential detection rate hypothesis versus the apparent-size selection hypothesis, explored the role of decision, and proposed a 'past detection rates model'. In laboratory feeding trials with bluegill sunfish, he manipulated turbidity in order to control the number and proportion of two *Daphnia pulex* size classes (1 and 2 mm, added at the same initial density: 14 individuals per liter) detected simultaneously by a fish. Gardner tested two alternative mechanisms: (a) the fish consumes zooplankton as detected, without making decisions: the larger sizes being eaten more frequently because of a perceptual bias (Eggers, 1977; Miller, 1979), or (b) the fish decides to ignore or pursue detected prey: the larger sizes being actively selected (Eggers, 1977).

Differential rates of detection, pursuit, or capture may generate a size-biased distribution of prey in the fish gut. At equal density of all prey sizes the fish detect a greater proportion of larger zooplankton. Thus, detection rate increases with prey size. This perceptual bias towards larger zooplankton requires no decision by the fish. Alternatively, the fish may ignore smaller zooplankton. This decision, at the pursuit step, results in an active selection towards larger zooplankton. The pursuit probability increases with prey size, or apparent-size (Vinyard & O'Brien, 1975; O'Brien *et al.*, 1976; O'Brien, 1979). But, the fish's decision to ignore or pursue upon detection induces differential pursuit rates for similar-sized prey (O'Brien, loc. cit.). Because capture ability of crustacean zooplankton is independent of prey size (Werner, 1974), it cannot cause size selectivity, but determined well the differential selectivity between taxa: e.g., copepods versus cladocerans (Allan, 1976; Drenner *et al.*, 1978).

Increasing turbidity level makes reactive distances decreasing and becoming independent of prey size (Ware, 1971; Vinyard & O'Brien, 1976; Eggers, 1977). In highly turbid water, the probability of simultaneous prey detection is very low, and the fish detects prey in the proportions of their actual size class distributions in the water column. Gardner (loc. cit.) observed that turbidity does not have a significant effect on the size selectivity of bluegill, but have a significant effect on the mean total num-

ber of *Daphnia* eaten by a fish during a three minutes trial (43 prey in clear pools: 1 NTU, and 22 prey in the most turbid pools: 190 NTU). Because the number eaten is proportional to the number detected, size selectivity is independent of the number detected (i.e., density, as perceived by the fish). Thus, when several prey are detected simultaneously, the detection rate and the feeding rate are not proportional to the reactive volume, but to the volume of water actually searched. To compensate partially for the reduced reactive distances in turbid waters the fish can increase its swimming speed. As, at the prey size range used (1 to 2 mm), the capture ability of *Daphnia* is independent of size, and size selectivity is not due to differential detection rate, Gardner concluded, as Werner & Hall (loc. cit.), that size selectivity is caused by the fish decision to ignore small 1 mm *Daphnia* upon detection. Since, (1) even when *Daphnia* is detected one at a time the fish still selects by size, and (2) selectivity does not decrease with decreasing number of simultaneously detected prey, Gardner disagreed with O'Brien *et al.* (loc. cit.) that a fish could compare and select apparent largest prey appearing in its visual field.

Based on his results, Gardner suggested an alternative mechanism. The decision was established on the only reliable estimate of prey density available to the fish: i.e., past detection rates, implicitly used in several foraging models (Schoener, 1971; Werner & Hall, 1974; Charnov, 1976). When previous detection rates are very low, the fish has a low estimate of prey density and eats zooplankton as detected. When they are high, the fish has a high estimate and chooses to pursue only the larger zooplankton. Nevertheless, Gardner formulated two limitations. First, the prediction of these results by an optimal foraging model is equivocal, as only the larger 2 mm *Daphnia* should have been eaten in all experiments. But, the decline in selectivity after four minutes of feeding trials may suggest that change in diet breadth is not continuous with prey density, but is saltatory, and depends on the minimum threshold value of the detection rate for the larger *Daphnia*, as predicted by optimal foraging theory (Werner & Hall, loc. cit.; Pyke *et al.*, 1977). Second, the fish's judgment capability may be limited. As *Daphnia* are not perfect spheres, the fish may misjudge their sizes when the angle between its sight line and the *Daphnia* broad side is

too large. Thus, the constant but biased selectivity pattern may represent a consistent error in the fish's evaluation of detected prey: that remains to be tested.

Janssen (1982) stressed that only one prey selection model may not be adequate for all fishes. Based on visual detection differences between a facultative planktivore, bluegill, and an obligate planktivore, blueback herring (see section III.A.1.), Janssen (*loc. cit.*) proposed an alternative 'first-sight model' in which bluegill pursues the first prey detected. This hypothesis is behaviourally simpler and consistent with previous works on bluegill feeding on *Daphnia* in which it is assumed that the fish inventories the prey, then makes a decision, choosing the most energetically rewarding prey to optimize energy intake, or choosing the largest apparent-sized prey (*i.e.*, the most likely to be detected first). Janssen underlined also that this proposal is different from a detection model, because bluegill will bypass potentially encountered prey as it pursues the first detected prey, and thus no choice is required.

While models of prey detection based on reactive distance versus prey size relationships are sufficient to predict the actual prey size-class frequencies in the fish diet (Ware, 1972; Werner & Hall, 1974; O'Brien *et al.*, 1976; Eggers, 1977; Gibson, 1980), models based on both actual reactive distances and volume-searched shapes are required to predict quantitative diets (Confer *et al.*, 1978). For a cruising fish, such as lake trout (*Salvelinus namaycush*), the reactive field (*i.e.*, the volume searched) is rather cylindrical and the prey detection rate is only proportional to the transverse visual plane area (Confer *et al.*, *loc. cit.*). For a fish, such as bluegill, which searches for each prey while stationary, the reactive field can be defined by detection probability profiles for various visual planes (Luecke & O'Brien, 1981). To elucidate the role played by the reactive field in the prey detection event, Dunbrack & Dill (1984) determined the scanning area (*i.e.*, the entire three-dimensional prey-reactive field) of juveniles coho salmon (*Oncorhynchus kisutch*). In nature, coho salmon feeds with its body almost stationary in running water, or actively searching in still water. The fish attacks prey, in most cases, ahead and above the horizontal plane. Thus, Dunbrack & Dill (*loc. cit.*) found the greatest reactive distances to be adjacent to the transverse plane

within and above the head portion of the visual field. The authors emphasized the use of the 'scanning area model' to predict diet composition, as it reflects not only the pattern of fish vision (*i.e.*, acuity and sensitivity), but also may reflect the skewed distribution of detected prey (as prey closer to the search trajectory are generally attacked before reaching the transverse plane) or the apparent increasing rate of prey movement which enhances the conspicuousness of those prey approaching the cruising fish.

Numerous studies have emphasized the role of various components in the alteration of the general pattern of size selectivity of visual planktivores on zooplankton communities, such as: the gape limitation for larvae and small species (Blaxter, 1966; Rosenthal & Hempel, 1970; Wong & Ward, 1972; Feller & Kaczynski, 1975; Guma'a, 1978; Furnass, 1979; Hunter, 1979), the role of prey visibility (Zaret, 1972; Ware, 1973; Zaret & Kerfoot, 1975; Kerfoot, 1980), prey motion and escape (Zaret, 1980; Kerfoot *et al.*, 1980; Vinyard, 1980), adaptive responses of prey (vertical migration, helmet development, reduced pigmentation) (Zaret, 1972b; Zaret & Suffern, 1976; Eggers, 1978; Hairtson, 1980; Wright *et al.*, 1980; Fraser & Cerri, 1982), the dependence on light and turbidity (Vinyard & O'Brien, 1976), the effects of hunger and prey density (Ware, 1972), the effects of experience (Ware, 1971), the effects and advantages of schooling (Eggers, 1976).

So, at present, the generally referred 'size-selective predation hypothesis' appears to be a simplified approach to the more complex process controlling prey selection by visual planktivores. It is evident that fish can discriminate between large and small prey, but it is not through direct size perception. The 'visibility-selective predation hypothesis' supported by Zaret (1980) is based on both optical properties of objects in underwater environments and visual acuities of fishes. The vulnerability of a prey to a particulate feeder is determined by both its inherent total visibility (which is mainly influenced by the more visible part of the body and the motion pattern; the prey escape ability is secondary because, by learning to recognize prey, visual planktivores can reach high capture efficiencies), and the range of visual acuities of the fish in the present light conditions of the aquatic environment (which is mainly influenced by its

spectral sensitivities and its contrast perception thresholds).

The Holling's predation-act model implies that, for particulate feeders (larvae and small species, as well as post-larvae: juveniles and adults), the probability of ingestion of a prey type i (I_i) is defined by the product of four conditional probabilities (with always $V_i = I_i \cdot D_i$

$$I_i = d_i \cdot p_i \cdot c_i \cdot r_i$$

where d_i , p_i , c_i , and r_i are the probabilities that the prey type i is detected (i.e., encountered in the visual field), pursued, captured (in the buccal cavity), and retained (on the branchial apparatus), respectively.

The probability d_i accounts for the differences between prey in size, shape, inherent contrast, contrast with the background, color (i.e., pigmentation), and motion behaviour. It is quantified by the reactive distance (RD_i) at which each a prey type i is detected. For each prey type RD_i varies with the illumination of the water.

The probability p_i reflects the decision of the fish to ignore or pursue detected prey. According to the model adopted, its calculation is based on past detection rates, apparent-size, or net rates of energetic intake. The decision may be influenced by the fish hunger level, and by its previous experience of prey (i.e., searching image concept). But, it may requires no decision by the fish if the first-sight hypothesis is used.

The probability c_i accounts for the differential escape ability of prey, and represents the fish capture efficiency for each prey type.

The probability r_i evaluates the retention capabilities of the branchial basket. It is estimated roughly by the value of the cumulative frequency of inter-raker (or intermicrobranchiospine) spacings corresponding at the size of the prey type i , and corrected for differences between similar-sized prey in shape, surface properties (relative to the filter), and palatability, on the functional characteristics of the filter (i.e., stickiness, and possible adaptative alterations of the mucus secretion rate; mesh size, and its possible mechanical or behavioural adaptative alterations), and on the characteristics of the water current passing over the entrapment structures (i.e., strength and direction).

The digestion probability of a prey type i (D_i) represents the digestion efficiency of this prey type

by the fish (i.e., the proportion of digested prey upon ingestion).

For particulate feeders, the detection rate (DRI) determines the maximum (i.e., potential) rate at which a prey type i is available to the consumption by the fish. DRI is the product of the prey environmental density (ED_i) by the square of the reactive distance (RD_i) of the fish for this prey (at the actual illumination and turbidity levels of the water environment), by the fish swimming speed during search (SSs), and by its searching frequency (SF):

$$DRI = ED_i \cdot RD_i^2 \cdot SSs \cdot SF$$

The searching frequency (i.e., the proportion of time spent foraging dedicated to searching) is the ratio:

$$SF = Ts/Tf \text{ with } Ts = Tf - Th$$

where Tf = the time spent foraging, Ts = the time spent searching for prey, and Th = the time spent handling prey.

The detection rate (DRI), successively corrected by the fish 'relative preference' (PP_i , in %) for pursuit upon detection (through decision, or not, when no (i.e., effects of experience and hunger), or one or several prey types are detected simultaneously; this proportion depends on the model adopted: differential detection rates, past-detection rates, apparent-size, or first-sight), and efficiencies for capture (CE_i , in %), retention (RE_i), and digestion (DE_i), i.e., the proportion of individual prey type i digested), represents the predicted fish feeding rate (FRI) on the prey type i :

$$FRI = DRI \cdot PP_i \cdot DE_i \cdot RE_i \cdot DE_i$$

An optimal foraging approach, based on Werner & Hall's (1974), Pearson's (1974), Charnov's (1976), Mittelbach's (1981), Eggers' (1982), and Werner *et al.*'s (1983b), may be used to predict the optimal diet breadth (i.e., the optimal range of prey types eaten) by a given-sized fish. Similarly to these models, the net rate of energy gained by a particulate feeder foraging in habitat j (NE_j/Tf_j) is the ratio:

$$NE_j/Tf_j = [\sum_{i=1}^m (FRI_{ij} \cdot E_{ij}) - Cs] / [1 + \sum_{i=1}^m FRI_{ij} \cdot H_{ij}]$$

with $E_{ij} = (A \cdot EC_{ij}) - (Chi \cdot Hi_j)$

where NE = the net energy gained while foraging (in Joule), T_f = the time spent foraging (in second), FR_i = the feeding rate (but not the detection rate, unlike the mentioned models) for prey type i (in number per second), E_i = the energy gained while foraging on prey type i (in Joule), C_s = the energy cost for searching (in Joule per second), H_i = the handling time for prey type i (in second), A = the assimilable fraction of an individual prey type i (in %), EC_i = the energetic content of an individual prey type i (in Joule), and Chi = the energetic cost of handling prey type i (in Joule per second).

The optimal diet is determined by ranking prey types from highest to lowest NE_{ij}/T_f ratios, and adding prey types to the diet until the ratio NE_j/T_j is maximized.

The energetic costs of searching (C_s) and handling (Chi) can be estimated from fish oxygen consumption as a function of fish length, swimming speed (SS_s and SS_h, respectively), and water temperature; the energetic content of a prey type can be determined by converting the prey length to dry mass, and then multiplying by the appropriate energy equivalent (Mittelbach, 1981).

2. Tow-net filter feeders

For tow-net filter feeders, the Holling's predation-act model implies that the probability of ingestion (I_i) of a prey type i is defined by the product of only two conditional probabilities:

$$I_i = c_i \cdot r_i$$

where c_i and r_i are the probabilities that the prey type i is captured and retained, respectively.

Since tow-net filter feeders do not provoke water pressure disturbances ahead while foraging at, generally, high swimming speeds (see section III.B.1.), it is probable that the capture event cannot cause selectivity. So, the prediction of particle selection by tow-net filter feeders may be reduced to the only assessment of the retention efficiencies of their branchial filters. Nevertheless, very few attention has been paid to the modelling of this feeding mode.

Extrapolated from Boyd's (1976) and Nival & Nival's (1976) analysis of the particle selection by

filter-feeding copepods, the filtering efficiency of a (tow-net or pump) filter-feeding fish can be estimated from the cumulative frequency of its interraker spacings. The simple sieving model is assumed, and then tested as a null hypothesis. The distances between gill rakers are measured, and used to build a cumulative frequency of interraker spaces. When rakers are elongated and nude (as in several clupeids), the interraker spaces may, more accurately, be weighted by the raker length (Drenner, 1977). Drenner *et al.* (1984a), using two gizzard shad (13.6 and 16.3 cm SL) pump filter feeding in a 80 liter pool, determined that the proportion of artificial spherical particles removed by fish increases as a function of particle size, leveling off at about 60 μm . They showed that the selective ingestion of these particles by gizzard shad can be predicted using a model of cumulative frequency of interraker distances. In similar feeding experiments using polystyrene microspheres ranging from 7 to 52 μm in diameter, Drenner *et al.* (1984b) determined that four size classes of blue tilapia (*T. aurea*) between 4.3 and 18.7 cm SL, pump filter feed selectively on microspheres larger than 25 μm . But, for blue tilapia particle retention by gill rakers is secondary and, small mucus-covered microbranchiospines located in a single row on the second, third, and fourth gill arches, may first account for the efficient retention of small particles by cichlids (Gosse, 1955; Fryer & Iles, 1972).

Overlooking the spacing frequency distribution of the branchial filter of the tow-net filter-feeding Atlantic menhaden, Durbin & Durbin (1975) used another calculation of the filtering (i.e., retention) efficiency (FE $_i$) for several phytoplankton species differing in sizes. For each particle size i , the authors computed FE $_i$ as the ratio between the specific filtering rate (i.e., the water volume swept clear per unit of time: F_i , in liter per fish per minute) and the maximum filtering rate (i.e., the total volume of water passing over its gill rakers: F_{max}, in liter per fish per minute). F_i was the product of the tank water volume (V , in liter) by the specific feeding rate (FR_i , in number of particle size i ingested per fish per minute). FR_i was computed from the regression curve between the log particle-concentration and time. F_{max} was calculated as the product between the mouth opening area (MA) and the mean swimming speed of the fish (SS_f) during the foraging period.

Although not well documented, it is probable that the optimization of particle retention by tow-net filter-feeding plantivores, through behavioural or mechanical modifications of their filter, may play a role in their selective feeding. For example, the paddlefish can change its swimming speed which controls the velocity of the water flow in through its filter, and can control, through muscular contractions, its mesh size (Rosen & Hales, 1981). Filtration rates by other tow-net filter feeders can roughly be considered as constant, because swimming speeds during feeding are generally unchanging.

Thus, for tow-net filter feeders, the capture rate (CR_i) determines the maximum (i.e., potential) rate at which a prey type i is available to the consumption by the fish. CR_i is the product of the prey environmental density (ED_i) by the maximum filtering rate (F_{max}) of the fish:

$$CR_i = ED_i \cdot F_{max}$$

F_{max} is the product of the fish mouth opening area (MA) by its swimming speed during the towing sequences (SSt) and by the towing frequency (TF):

$$F_{max} = MA \cdot SSt \cdot TF$$

TF (i.e., the proportion of time spent towing during a foraging period) is the ratio:

$$TF = Tt/Tf \text{ with } Tt = Tf - Th$$

where Tt = the time spent towing, Tf = the time spent foraging, and Th = the time spent handling prey (i.e., the duration of the swallowing movements during which the food bolus is transported from the filter into the oesophagus).

The capture rate (CR_i), successively corrected by the fish efficiencies (in %) for retention (RE_i), and digestion (DE_i), represents the predicted fish feeding rate (FR_i) on the prey type i :

$$FR_i = CR_i \cdot RE_i \cdot DE_i$$

The net rate of energy gained by a tow-net filter feeder is computed from the equation used for particulate feeders, and the optimal diet is predicted by following the mentioned procedure.

3. Pump filter feeders

As for tow-net filter feeders, for pump filter feeders, the Holling's predation-act model implies that the probability of ingestion (li) of a prey type i is defined by the product of two conditional probabilities:

$$li = ci \cdot ri$$

where ci and ri are the probabilities that the prey type i is captured and retained, respectively.

Contrary to tow-net filter feeders, the capture event may well determine the selectivity of pump filter feeders (see section III.B.1.). The escape ability of prey determines the capture efficiency of pump filter feeders for zooplankton. But, non-evasive particles are captured in proportion to their densities in the environment, and selected only according to the fish retention efficiency.

Thus, for pump filter feeders, the capture rate determines, as for tow-net filter feeders, the maximum (i.e., potential) rate at which a prey type is available to the consumption by the fish.

The capture rate (CR_i) of a prey type i is the product of the prey environmental density (ED_i) by the maximum filtering rate (F_{max}) of the fish:

$$CR_i = ED_i \cdot F_{max}$$

An approach similar to Durbin & Durbin's may be used to predict the retention efficiency ($FE_i = Fi/F_{max}$) of a pump filter feeder for a prey type i without direct measurements of its filter. In this case, F_{max} can be computed from the product of the buccal pumping rate (PR) by the buccal volume (BV) and by the pumping frequency (PF) (Drenner *et al.*, 1982b):

$$F_{max} = BV \cdot PR \cdot PF$$

Contrary to tow-net filter feeders, F_{max} of pump filter feeders may not be completely considered as constant (Drenner, in litt.) because pumping rates may vary. Buccal pumping rates can be determined from films or video recordings, and buccal volumes (i.e., maximum suction volumes) by injection of plaster (Drenner, 1977; Drenner *et al.*, 1982b), silicone, or dentist casting past (such as, Geltrate® :Lazzaro, in progress). Drenner *et al.*

(loc. cit.) developed this pump filter-feeding rate model for 5–15 cm SL gizzard shad. Buccal volume is a (nearly cubic) power function of shad standard length, while pumping rate (determined from 16 mm films at 64 frames per second) declines exponentially. Filtering rate (in liter per minute) is a positive power function of shad standard length, but a negative power function of shad body weight. They tested the model during four 1.5 hour laboratory feeding trials with rotifers and nauplii. The prey densities declined exponentially with time. Actual and predicted densities were not significantly different. But, the authors emphasized that the predicted filtering rates are potential and not absolute measurements.

The pumping frequency (i.e., the proportion of time spent foraging dedicated to pumping) is the ratio:

$$PF = Tp/Tf \text{ with } Tp = Tf - Th$$

where Tf = the time spent foraging, Tp = the time spent pumping, and Th = the time spent handling prey. Contrary to particulate feeders which handle prey individually, tow-net and pump filter feeders stop towing and pumping, respectively, to handle simultaneously all organisms and particles constituting the food bolus trapped during the filtering sequence from the gill rakers, the microbranchiostomes, or the pharyngeal pockets into the oesophagus. For example, gizzard shad display unusually large 'swallowing' movements, between each pumping sequence (Drenner *et al.*, loc. cit.).

The capture rate (CRI), successively corrected by the fish efficiencies (in %) for retention (REi), and digestion (DEi), represents the predicted fish feeding rate (FRi) on the prey type i:

$$FRi = CRI \cdot REi \cdot DEi$$

The net rate of energy gained by a pump filter feeder is computed from the equation used for particulate feeders, and the optimal diet is predicted by following the mentioned procedure.

B. Optimal foraging predictions, habitat shifts, and feeding mode switches

By the past, numerous planktivore models have been developed in a rather quantitative way, be-

cause they were based on body size, which has been considered for a long time as the primary prey characteristic responsible for the selectivity of planktivores. Now, it is manifest that the consideration of (even empirical) information on a) other interactive prey characteristics, such as, visibility and motion (for particulate feeders), and escape ability (for filter feeders), b) previous fish experience for prey, c) fish hunger level, and d) fish capability for feeding mode switches and habitat shifts, are essential when attempting to make models more realistic. Flexibility limits often the realism of ecological models which may fail to predict changes a) in planktivore diet and in habitat use, as a consequence of plankton resource alterations, and b) in plankton communities induced by planktivorous fishes.

An example emphasizing the plasticity of the trophic interactions between planktivores and their food is done by Eggers (1982), who estimated the relative frequencies of various prey species and size categories occurring in stomach contents of Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*) at different seasons of the year. He showed that sockeye have a high, but extremely dynamic preference for large non-evasive prey, according to their seasonal availability in the water column. Small as well as evasive prey are pursued and captured during periods when large non-evasive forms are scarce or absent. He pointed out the extreme flexibility of prey preference by planktivorous fishes as an adaptative response to changes in prey composition.

Aquatic environments are generally heterogeneous. So, the expressions proposed for each planktivore feeding mode might include parameters accounting for the fishes ability to (visually) detect prey patches, and for their foraging strategies (e.g., feeding mode switches, when behaviourally available, in response to changes in the food resources of the environment) in discriminating between patches and using them. Theory of habitat 'patch' use are based on empirical studies where an experimental habitat of homogeneous structure includes areas of different prey densities (e.g., Krebs *et al.*, 1974). Most foraging models dedicated to habitat uses by freshwater planktivores concern particulate feeders, and almost exclusively bluegill sunfish, *Lepomis macrochirus*. In contrast, the selective advantage of the filter feeding modes (in term of net energy

gained by foraging this way towards that gained by particulate feeding) remains still little explored.

Using a statistical approach based on a stepwise regression analysis, Lammens (1985) developed a conceptual model of pump filter feeding bream, *Abramis brama*. Comparing stomach contents of 9–35 cm SL bream and zooplankton samples collected from a small shallow eutrophic lake, he tested three hypotheses: a) the average prey size increases with bream length, while standard deviation declines, b) the prey size is strongly correlated with available prey size, and c) the prey density has little effect on prey size selection (i.e., clogging of the gill rakers does not occur). Lammens (loc. cit.) demonstrated that the three assumptions cannot be rejected for bream pump filter feeding on 0.36–0.56 mm *Bosmina coregoni*, and for bream larger than 20 cm SL pump filter feeding on 0.90–1.52 mm *Daphnia hyalina*. For bream smaller than 20 mm SL feeding on *D. hyalina*, all assumptions were rejected because the fish use particulate feeding or a combination of particulate and pump filter feeding. Thus, as stressed by Lammens for bream, it is urgent to develop foraging models combining particulate and filter feeding and including the ability to switch between feeding modes. Built-in switching mode procedure, in response to spatial or temporal changes of plankton composition and density in the fish environment, will improve model predictions.

Quantifying the cost of feeding on prey (i.e., the handling time per prey weight) for particulate feeding alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) and for alewife using a combination of particulate, gulping and filtering modes, Crowder & Binkowski (1983) examined the energetic advantages of feeding mode switches. Fish were fed *Daphnia* and *Mysis* in laboratory experiments. Cost curves for particulate feeding bloater and alewife are very similar. They are lowest for the largest prey available in the open lake (*Mysis*) and increase exponentially for smaller prey. But, if alewife cost curves are adjusted for switches in feeding mode (i.e., gulping, filtering), as observed to occur by Janssen (1976), relative costs of feeding on small prey are much reduced.

Feeding mode switches in alewife are correlated with relative time costs of particulate feeding versus filter feeding. Whereas alewife can switch from particulate feeding to filter feeding, bloater appar-

ently cannot (Janssen, 1976, 1978a). If the size of prey is small relative to that of the fish and their density sufficiently high, filtering may be more profitable than particulate feeding. Only the largest alewives (30 g) filter feed (Janssen, 1976). But, small alewives (50–70 mm SL) may filter in the field at dusk (Janssen, 1978b). Actually, filter feeding may be more frequent at night (Janssen, 1978b, 1980) because, as light levels decline, the size of the visual field and the detection rates of prey decrease (Vinyard & O'Brien, 1976) and the selective advantage of switching to filtering should increase (Holanov & Tash, 1978).

The use of different feeding modes is dependent upon prey-predator size ratios, prey density, and the ability to switch feeding modes. For example, whereas menhaden particulate feed on larger prey (prey size/fish size ratios from 1/20 to 1/200), they filter feed on smaller prey (ratios from 1/50 to 1/20000) (Durbin, 1979).

Crowder & Binkowski (loc. cit.) suggested the existence of a switching competitive balance between alewife and bloater as, if prey sizes shift towards smaller prey, alewife could take advantage over bloater due to their ability to profitably switch to filter feeding on these prey. Using Janssen's (1976) data on alewife, they showed that, at an experimental density of 254 *Daphnia* per liter, a) handling time per prey increases from small (0.068 mg wet weight) to large (0.241 mg wet weight) *Daphnia*, and from filtering, to gulping, and then particulate feeding, b) the feeding rate on small *Daphnia* (0.068–0.70 mg wet weight, 0.020–0.026 10^4 fish-prey weight ratio) is the highest (13.65–14.57 *Daphnia* eaten per second, 0.95–0.99 mg dry weight eaten per second), when the filter feeding mode is used, c) the feeding rate on large *Daphnia* (0.205–0.241 mg wet weight, 0.180–0.301 10^4 fish-prey weight ratio) is the lowest (1.98–2.32 *Daphnia* eaten per second, 0.48–0.51 mg dry weight eaten per second) when the particulate feeding mode is used, whereas d) the gulping mode used to feed on intermediate-sized *Daphnia* (0.124–0.160 mg wet weight, 0.055–0.124 10^4 fish-prey weight ratio) provides intermediate feeding rates (3.10–4.73 *Daphnia* eaten per second, 0.46–0.65 mg dry weight eaten per second).

Because most optimal foraging models of planktivorous fishes are based exclusively on the particulate feeding mode although many obligate plankti-

vores also filter zooplankton, Crowder (1985) hypothesized that feeding mode switches may be predictable from the costs and benefits of foraging in various modes. As in fishes that switch feeding modes, small individuals generally particulate feed whereas large individuals filter feed (Leong & O'Connell, 1969; Janssen, 1976; Holanov & Tash, 1978; Durbin, 1979; Drenner *et al.*, 1982c), Crowder (loc. cit.) pointed that the different feeding modes may be dependent on both the fish-prey size ratio, the relative densities of large and small prey, and the ability to switch feeding modes.

To support his hypothesis, Crowder (loc. cit.) analyzed three quantitative examples of switch from particulate feeding to filter feeding. For each independent case, he noted a surprising agreement between the feeding mode switch observed and the relative profitability of each mode.

First, using Leong & O'Connell's (1969) data on Northern anchovy, *Engraulis mordax*, feeding on various densities of *Artemia* nauplii and adults, Crowder (loc. cit.) determined the equal return rate isopleth (i.e., the curve representing the combined densities of adults and nauplii which would provide an equal return rate (mg dry wet per minute) to an anchovy filtering nauplii or particulate feeding on adults). Plotting on the same graph the percent of observations in which schooling anchovies were particulate feeding on various densities of adult *Artemia*, in tanks containing an average of 200 to 400 nauplii per liter (O'Connell, 1972), Crowder noted that the isocline for 50% particulate feeding is closely parallel to the isopleth of equal return rates. This demonstrated that feeding modes at different densities of large and small prey may be accurately predicted by optimal foraging theories. However, the response is graded as, when filter feeding should be more profitable, some particulate feeding is observed and conversely.

Second, using similar experimental data on Pacific mackerel, *Scomber japonicus* (O'Connell & Zweifel, 1972), Crowder (loc. cit.) determined that a density of 2.007 adult *Artemia* per liter should provide equal return rates through particulate or filter feeding. Again, this density predicted by an optimal foraging hypothesis is close to that (1 or 2 *Artemia* per liter) derived from observations and intuition of O'Connell & Zweifel (loc. cit.).

Third, considering comparable data on alewife, as a) when the cost curve (Werner, 1977) is adjusted

for switches in feeding modes the relative costs of feeding on small prey is much reduced (Crowder & Binkowski, 1983), and b) in tanks with known sizes and densities of zooplankton (Janssen, 1976), large fish (30 g) filter feed, medium-sized fish (12.7–22.5 g) gulp, and small fish (8.0–12.9 g) particulate feed, Crowder (loc. cit.) assumed that the cost curves may well explain the feeding mode switch observed to occur near the prey-fish weight ratio for which the cost curve including filtering has a lower cost/benefit ratio than that for particulate feeding. Nevertheless, as a) the actual energetic costs of filtering versus particulate feeding are poorly known (Durbin, 1979), b) the costs of swimming while filtering might be slightly higher, and c) the threshold value of the prey-fish weight ratio inducing feeding mode switch must certainly depend on prey density, Crowder emphasized that this assumption still need additional testing.

Besides, as microscale patches in zooplankton are frequent and average zooplankton densities are significantly lower than densities found in patches (Steele, 1974; McNaught, 1979; Owen, 1981), Crowder stressed that patchily distributed zooplankton may frequently support filtering and it would be very advantageous for fish to be able to rapidly switch back and forth between feeding modes to forage in such patchily environments. Finally, he remarked that by comparing plankton yields, using alternatively particulate and filtering modes, fishes may be able to assess better which provides the greatest net energy gain. He concluded that including feeding mode switches (based on optimal foraging theory) in models, to respond to spatial and temporal patchiness (i.e., to account for both effects on detection rates and sampling between modes), should improve their predictions.

A main goal responsible for the expansion of optimal foraging theories in prey selection models is the prediction of planktivore diet and habitat use as a function of food resource availability and benefit for the fish. This knowledge has a potential relevance to the study of aquatic community interactions in lakes. It represents a potential basis to support mechanistic theories of competition and species packing for the prognosis of aquatic community structures (Werner, 1977).

Studying the ecological segregation between three sunfish species in small ponds, Werner & Hall (1976) disclosed that, as segregation increases with

resources decline, and niche shifts depend on the presence of congeneric sunfishes, experimental studies of foraging behaviour mechanics are essential to understand the organization of aquatic communities. To identify the competitive mechanisms responsible for habitat shifts of bluegill sunfish in presence of a congener, green sunfish (*Lepomis cyanellus*), Werner & Hall (1977) confined each species alone and with the congener in homogeneous patches of vegetation habitat. Morphological and behavioural attributes permit bluegill to exploit a broader array of habitats (Keast, 1970; Werner & Hall, 1976; Werner, 1977; Werner *et al.*, 1977), although their more protrusible mouth are more efficient in capturing small zooplankton. This habitat flexibility eclipses the competitive advantage of the sit-and-wait foraging behaviour of green sunfish in vegetation environment. As the mechanisms involved in habitat shifts among centrarchids are similar to those applying among salmonids (e.g., between allopatric populations of brown trout, *Salmo trutta*, and arctic char, *Salvelinus alpinus*, in Sweden: Nilsson, 1960, 1963; between trout, *Salmo clarki*, and char, *Salvelinus malma*, in sympatric and allopatric populations in Canada: Andrusak & Northcote, 1971, and Schutz & Northcote, 1972), Werner & Hall (loc. cit.) stressed that studies documenting habitat shift and partitioning are essential to understand aquatic community assemblages.

Werner *et al.* (1981) demonstrated that fish learning (i.e., experience related effects) can readily alter the predictions of foraging models. Thus, they recommended to explore the various mechanisms involved and include them in models of prey selection, in order to improve habitat use predictions and test submitted theories. In field tests of an optimal foraging model, Mittelbach (1981) and Werner *et al.* (1983a) demonstrated the importance of the size-related predation risk for differences in habitat use between various size classes of bluegill sunfish.

Werner & Hall (1974), Mittelbach (1981), and Werner *et al.* (1983b) demonstrated that bluegill sunfish can respond to changes in the resource level of the environment by modifying their food particle size selection, in close agreement with predictions by foraging models. Similarly, Werner (1982) and Werner *et al.* (1983b) showed that habitat shifts by bluegill in small ponds, as a consequence of

changes in the resource levels of these habitats, can be predicted by foraging models. Applying the optimal foraging approach to the study of fish feeding behaviour, Werner *et al.* (1983a, 1983b) explored the capabilities of bluegill sunfish to assess short term changes in their environment, and their flexibility to respond to these changes in ways predicted by the model. The optimal foraging model (which conceptualization is developed in Mittelbach, 1981), based on detection rates versus prey size and density, and fish length, plus the laboratory assessment of foraging costs, permitted Werner *et al.* (loc. cit.) to predict actual food selection within habitats, as well as, foraging rate differences between three habitats (open water, sediments, and vegetation). Deviations from predictions of the model allowed them to discover additional mechanisms controlling the prey preference by bluegill. Even, the accurate predictions of the size-frequency distribution of *Daphnia pulex*, as a function of the fish body length, made the authors suggested that the size-selective predation by bluegill may be related to 'some energetic considerations' by the fish. Nevertheless, slight changes in the estimated prey detection rates or prey densities can alter the accuracy of the diet prediction. Thus, Werner *et al.* (loc. cit.) stressed that the assessment of the zooplankton densities actually experienced by the fish while foraging is a crucial need.

As, in natural lakes, small bluegill are restricted to weedbeds and their foraging rates conflict with those predicted by optimal habitat use models (Hall & Werner, 1977; Mittelbach, 1981), Werner *et al.* (1983a) postulated that the predation risk exerted by piscivorous largemouth bass (*Micropterus salmoides*) is responsible for this deviation from predicted foraging behaviour. The presence of bass caused vulnerable small size classes of bluegill to forage in less profitable, but safer, vegetation habitat. These data provided experimental support for the hypothesis of Hall & Werner (loc. cit.) and Mittelbach (loc. cit.) that small fishes are limited to weedbeds because of a behavioural response to the greater predation risk suffered in more open habitats. Nevertheless, the cues used by fish to evaluate the predation risk are unknown. Werner *et al.* (loc. cit.) noted that predation risks tend to concentrate the young of many fish species in the vegetation of natural lakes (Hall & Werner, loc. cit.; Laughlin & Werner, 1980; Mittelbach, 1984). So,

they suggested that competition and predation may interact in subtle, but critical ways, in fish communities.

In conclusion, field (or laboratory) tests of foraging models are essential to evaluate the knowledge of mechanisms involved in the selective (or random) use of plankton by planktivorous fish. More studies are needed to explore the (ecological, physiological, or behavioural) cues used by fish to assess short term change in the relative resource levels of their habitats. Predictions of diet and habitat use of individual fish should help to determine potential changes in plankton (and other aquatic) communities that could be generated by fish populations. In addition, models of prey selection and habitat use might include input variables (rather than state-variables, as suggested by Bakule & Straškraba, 1982) to mimic optimization constraints (such as, influences of previous experiences for the various food types, hunger level, intra- and interspecific competition for resources, predation risk from upper trophic levels, on feeding behaviours within habitats and foraging patterns between habitats) to improve their soundness.

It means that models must modulate their responses (i.e., feeding modes, rates, and selectivities, feeding mode switches, foraging patterns, habitat shifts) to changes in the environment, by adapting their own structures to new constraints, just as natural systems do. For example, when particulate feeding within an habitat is no more beneficial for the fish (because the energy gained by feeding this way does not compensate the costs, or the presence of piscivores in this habitat makes too dangerous to feed this way during the day), is it more profitable (in the sense of optimizing the fish diet breadth) to shift habitat (i.e., to continue particulate feeding in an habitat of higher profitability, or lower predation risk, respectively), or to remain in this habitat but switch feeding mode (i.e., to use filter feeding in that habitat if it is more beneficial for increasing the net energy gained, or to avoid predation in that habitat by filter feeding at night, respectively)? Such alternatives might be investigated, using a mechanistic approach similar to Holling's. Feeding mode switches and habitat shifts could be predicted by comparing actual past detection rates for particulate feeders (Gardner, 1981) or past 'swallowing' rates for tow-net and pump filter feeders (i.e., the rates at which towing and pumping are interrupted

to transport the food bolus from the branchial apparatus into the oesophagus) to reference threshold values. Past detection rates (Gardner, 1981) and past swallowing rates are probably the only reliable estimates of prey density available to the fish.

Preliminary feeding behaviour experiments with the concerned fish are essential to determine if the foraging model must incorporate tow-net and/or pump filter feeding in addition to particulate feeding, and procedures for feeding mode switches in addition to procedures for habitat shifts. The knowledge of the feeding mode repertory permits to explore all the alternatives available to the fish to maximize its net energy gained while foraging. As the feeding mode repertory depends generally on the fish age, a foraging model may not be valid for the entire life of a single fish. This has considerable consequences for modelling the habitat use by fish populations (see also the effects of schooling on feeding mode and selectivity in section II.D.). To predict feeding mode switches, it remains to establish in which circumstances and habitat types tow-net and pump filter feeding have the selective advantage over particulate feeding to increase the fish diet breadth. Apart from improving the flexibility and realism of fish foraging models, such studies should give very interesting insights about the driving forces responsible, through natural selection, for the differentiation and the fitness of the various feeding modes used by planktivorous fish.

We now have substantial evidences that fish forage on plankton in an 'optimal-like way'. Thus, it appears pressing that future models of prey selection by planktivores should include both habitat shift and feeding mode switch abilities, together with changes in feeding mode repertory following fish growth (i.e., size). This is essential for modelling accurately plankton selection by planktivore populations.

VI. Field evidence of planktivorous fishes selective impact on plankton communities

A. Impact of particulate feeders

1. Direct effect on zooplankton communities

Ivlev (1961), summarizing ten years of Russian fish feeding research (and mostly on non-planktivores), first presented evidence for the im-

portance of prey size to fish predators. According to Novotna & Korinek (1966), the pioneer works exploring in experimental ponds the effects of the fish stock on the zooplankton composition and abundance were realized by Walter (1895), Contag (1931), Pliszka (1934), Weimann (1938, 1939, 1942), and Susta (1938), whereas the changes in plankton communities induced in a lake by the concentration of the fish population, consecutive to a drop in water level to half its optimal value, was studied by D'Ancona & Volterra D'Ancona (1937). However, Hrbáček *et al.* (1961) definitively showed, in small European carp ponds, that zooplankton species composition and size range was influenced by the predation pressure of planktivorous fishes. Later on, Brooks & Dodson (1965) concluded that the introduction of marine planktivorous alewives (*A. pseudoharengus*) into small southern New England lakes caused marked changes in zooplankton composition. By comparing the zooplankton distributions of some of these lakes, the authors demonstrated that (1) large zooplankters were particularly vulnerable to predation by alewives, and (2) as a consequence of this piscine planktivore predation, alewife lakes were characterized by the absence of large zooplankters (see Fig. 9). Thus, they proposed that selective predation by alewives results in the elimination of the larger zooplankters more

susceptible to fish predation, and their replacement by smaller, less vulnerable, forms. The studies of Hrbáček *et al.* (loc. cit.) showed the same selective pattern in carp ponds, and the authors hypothesized that the changes observed in the zooplankton composition were the result of size-selective feeding by carp.

These papers have been followed by a great number of publications emphasizing the size-related alterations in zooplankton communities as a consequence of planktivorous fishes. In Lake Albert, Green (1967) related the differential selection of planktivores for two prey morphs of *D. lumholtzi* to a difference in prey body size. Hall *et al.* (1970) observed shifts towards smaller sizes of zooplankton following bluegill introduction into experimental ponds. The replacement of larger *D. pulex* by smaller *D. dubia* as a consequence of smelt (*Osmerus mordax*) introduction was observed by Reif & Tappa (1966) in Harvey's lake, Pennsylvania.

Selective predation by alewives in Lake Michigan resulted not only in the decline of the largest calanoids, and cladocerans, but also in the decrease of the average size and the size at onset of maturity of *D. retrocurva*, while smaller species increased in number (Wells, 1970; see Fig. 10). In the same manner, a shift in zooplankton size distribution towards smaller forms, plus a decrease in size and minimum egg-bearing size of *D. galeata* were consequences of alewife introduction in Lake Wononskopomuc, Connecticut (Warshaw, 1972). 'Size-selective' rainbow trout (*S. gairdneri*) and yellow perch (*P. flavescens*) introduced into two Michigan lakes, fed only upon *Daphnia pulex* over 1.3 mm long, which are mature, as well as immature in Sportley Lake, and are mostly mature in Stager Lake (Galbraith, 1967). Thus, predation on *Daphnia* can be considered age specific as well as size specific. In Sportley Lake (see Fig. 11) the daphnid population was dramatically affected by the fish introduction (complete elimination of *D. pulex*, progressive replacement by two smaller species, decrease in average size of daphnids from 1.4 to 0.8 mm, decrease in percentage of daphnids larger than 1.3 mm from 53.8% to 4.7%) but in Stager Lake none of these changes occurred. Galbraith's results pointed out the necessity to consider the maturation size of daphnids for interpreting trophic relationships between daphnids and planktivorous fishes.

Comparing the populations of *Daphnia cucullata*

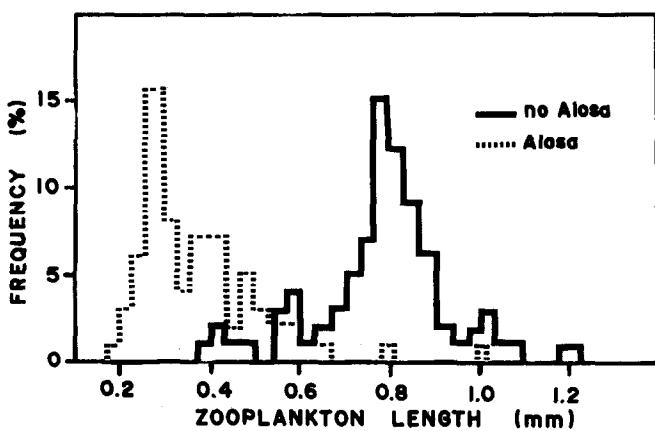


Fig. 9. Mean size of zooplankton in Crystal Lake, comparing ten years before the introduction of *Alosa aestivalis* (Clupeidae) with ten years after: the usual large-sized crustacean dominants (spp. of *Daphnia* and *Diaptomus*: respectively 1.3 and 0.8 mm long) are eliminated and replaced by small sized, basically littoral species (especially *Bosmina longirostris* 0.3 mm long) (from Brooks & Dodson, 1965).

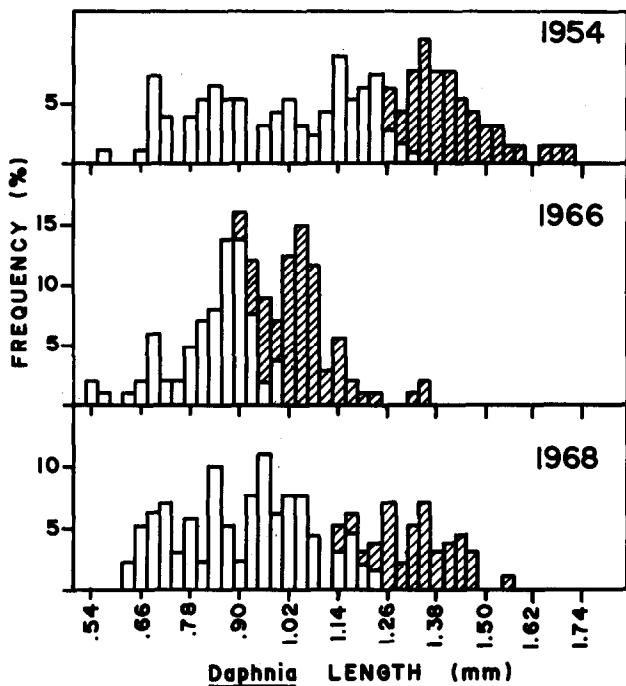


Fig. 10. Length distributions of female *Daphnia retrocurva* from Lake Michigan samples of 1954, 1966 and 1968 (darkly shaded portions represent mature individuals) (from Wells, 1970).

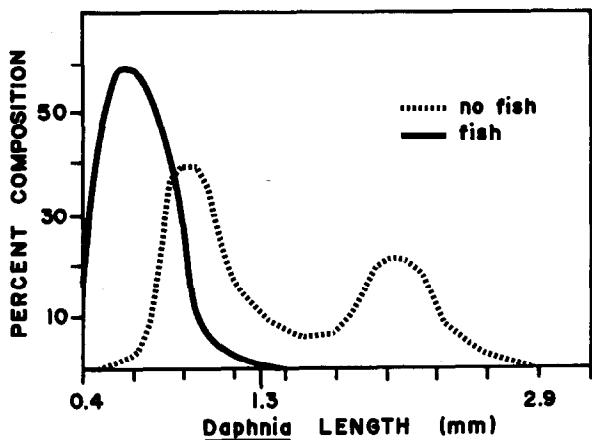


Fig. 11. Size frequency distribution of *Daphnia* in net plankton of Sportley Lake during toxaphene treatment toxic to fish (September, 1958), and five years after rainbow trout (*Salmo gairdneri*) introduction (September, 1964) (from Galbraith, 1967).

ta in two eutrophic Mazurian lakes (Southern Poland), Gliwicz *et al.* (1981) showed that a smaller mean individual size and a younger age structure in (predation dominating) Lake Mikolajskie contrasted with a larger mean individual size and an older age structure in (food concentration limiting) Lake Majcz. They observed a decreased clutch size (i.e., mean number of eggs carried per female) in the larger size classes of *Daphnia* populations as a consequence of the selective removal of the (more conspicuous and less evasive) larger females carrying a greater number of eggs and the females of the same size (age) class carrying greater number of eggs. Plotting the body length versus the average or maximum clutch size of various cladoceran species of daphnids and sidids, Gliwicz (1981) determined that, for similar body lengths, cladocerans typical in lake epilimnia have their clutches smaller than those of cladocerans common in small and fishless water bodies. Because this was also true for cyclopids and calanids, Gliwicz emphasized that selective predation by visual planktivores should be considered as a determinant factor controlling the clutch size in planktonic crustaceans. As Zaret (1972b; see section III.A.1.) speculated that eggs or ephippia production was probably related to predation pressures, Gliwicz (loc. cit.) gave an alternative interpretation to Zaret's work concerning the fish selective removal of the more conspicuous cyclo-morphic morph of *Ceriodaphnia cornuta*. Not only its larger compound eye, but also its four times greater clutch size could be responsible for the greater vulnerability of the unhorned morph to visual planktivorous fishes, against the horned morph.

But, both food limitation and selective predation may induce a decreased mean number of eggs per female and a decreased fecundity of a cladoceran population (Gliwicz, loc. cit.). So, Gliwicz *et al.* (1981) stressed that the entering reproduction by smaller cladoceran females may be rather a long-term evolutionary strategy than a demographic response of a cladoceran population to an increase in planktivorous fish predation pressure (Galbraith, 1967; Wells, 1970). An increase in planktivorous fish predation induces better food conditions. It results in an increase in the fecundity of younger cladoceran instars which enter earlier in reproduction. Comparing the population dynamics of cladocerans in Lake Mikolajskie inhabited by rich

populations of planktivorous fishes and in a fish free pond, Dawidowicz & Pijanowska (1984) suggested that planktivorous fishes might be the main factor responsible for the different patterns of cladoceran abundance. They showed that the competitive exclusion principle (i.e., species with similar ecological requirements are not able to co-exist in a stable environment: Hardin, 1960), which seemed realized in the pond, was not supported in the lake. The planktivorous fishes, by selectively removing the best competitors (i.e., the larger zooplankters), reduce the interspecific competition within zooplankton and allow a few cladoceran species to reach their highest densities simultaneously, thus disregarding this principle.

In shallow plastic pools, Hurlbert *et al.* (1972) observed that, in less than three months, the mosquitofish (*Gambusia affinis*) eliminated insects (benthic chironomid midge larvae, surface nymphs of the mayfly family Baetidae, and surface larvae and pupae of the Diptera family Ephydriidae) and *D. pulex* populations. Moreover, the fish significantly reduced populations of the rotifer *Brachio-*

nus quadridentata. In control pools (without fish) insects and *D. pulex* became abundant. In experimental ponds, Hurlbert & Mulla (1981) found that predation by mosquitofish produced a shift towards smaller species of rotifers (from *Keratella quadrata* to *K. cochlearis*), as well as, a decrease in the calanoid/cyclopoid ratio (from *Diaptomus pallidus* to *Cyclops vernalis*). As Brooks (1968) suggested that the erratic jumping motion of cyclopoids is more conspicuous to fish than is the typically gliding motion of calanoids, an increasing calanoid/cyclopoid ratio might be expected as a result of *Gambusia* predation. To explain the difference between the observed change in calanoid/cyclopoid ratio and the expected one, Hurlbert & Mulla (loc. cit.) assumed that the increased survival of predaceous cyclopoid copepodites (as a consequence of *Gambusia*'s selective predation on adult cyclopoids) resulted in a greater selective removal of calanoids over cyclopoids (see Fig. 12).

Decline in abundance or removal of planktivore populations induce generally a partial reversal of

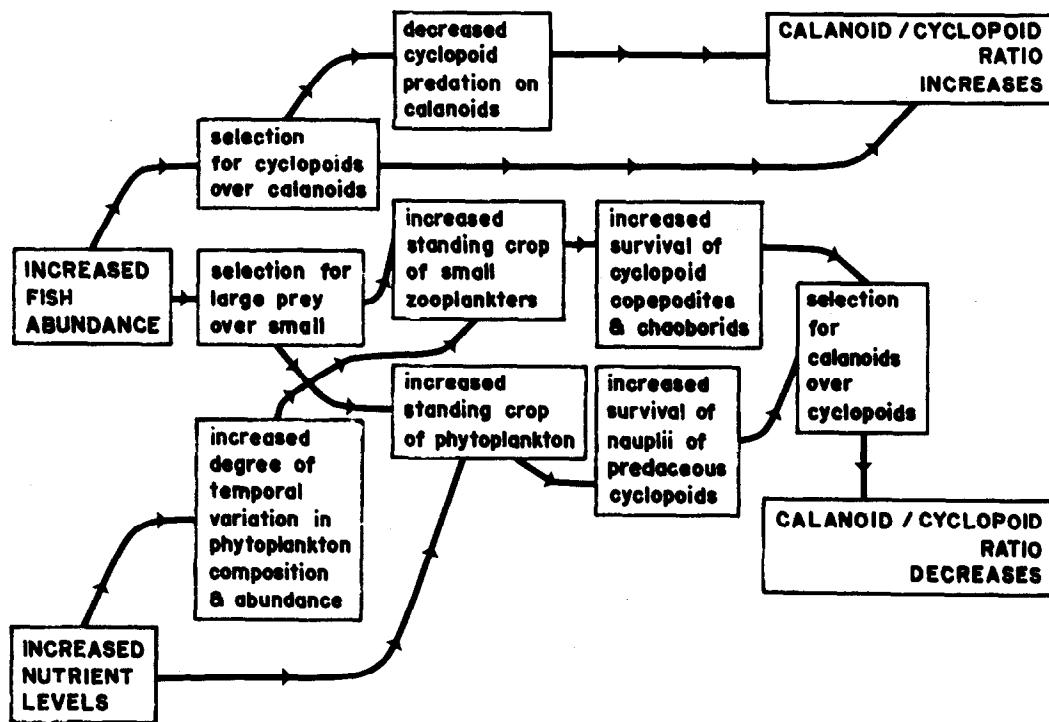


Fig. 12. Some principal ways in which the ratio of calanoid to cyclopoid copepods is influenced by zooplanktivorous fish, predaceous zooplankters, and nutrients (from Hurlbert & Mulla, 1981).

the previous size distribution of zooplankton populations. Experiments (Hrbáček *et al.*, 1961; Hrbáček, 1962; Galbraith, 1967; Wells, 1970; Andersson *et al.*, 1978; Stenson *et al.*, 1978; Fott *et al.*, 1979; Shapiro *et al.*, 1982; Shapiro & Wright, 1984) in which fish were removed (by poisoning) from water bodies where zooplankton communities were initially dominated by smaller species, always produced a shift towards larger filter-feeding zooplankton (such as *Ceriodaphnia* spp.). Warshaw (1972) also observed an increase in the number of large zooplankton species (*Daphnia*, *Leptodora*, *Epischura*) following the die-off of *Alosa*.

Because zooplankters have short generation times, changes in their community structure and dynamics, in response to changing fish predation pressures, may be relatively quick. Grygierek (1962) showed that in carp ponds these changes occurred after a few weeks, whereas in Lake Warniak they took place during several months. Thus, Weglenska (1971) considered that the size and fecundity of resulting populations of crustaceans and rotifers can be used as sensitive indicators of trophic conditions in free waters.

It may be noticed that most studies have been devoted to the direct effect of fish visual predation on zooplankton. However, Hillbright-Ilkowska & Weglenska (1973) emphasized that not only direct fish selective predation was responsible for changes in zooplankton dynamics, but the indirect effect by means of habitat transformations also played a significant role. Following Brooks & Dodson (1965), they proposed that the disappearance of large herbivores (which have low production/consumption by fish ratios, such as, *Diaphanosoma* and *Eudiaptomus* species) from Lake Warniak was, as well, a consequence of the habitat being occupied by small, fast growing and quickly reproducing herbivores (such as, *Ceriodaphnia*, *Bosmina*, *Keratella* and *Polyarthra* species). The latter, filter feeding mostly on small suspended particles and bacteria, and not selectively removed by fish, were favoured by the increasing density of detritus resulting from the fish feeding activity. The authors concluded that the overall effect of increasing fish stock on zooplankton resulted in (1) the increase in density, biomass, production, fecundity and size of small filtering herbivores (i.e., cladoceran and rotifer species), (2) the decrease in density and biomass of large filtering herbivores (i.e., mainly large cladoc-

ran and calanoid species), (3) the increase in density, fecundity, biomass and production of predatory cyclopoids, and (4) the increase in the production rate of the overall zooplankton community.

In temperate zones, the dominance of small cladocerans (particularly, *Bosmina longirostris*, *Ceriodaphnia quadrangula*) and rotifers (*Keratella cochlearis*) usually follows a periodical or constant increase of fish stock (Hrbáček *et al.*, 1961; Hrbáček, 1962; Hillbright-Ilkowska, 1964, 1966; Grygierek *et al.*, 1966; Grygierek, 1967), and allows identification of water bodies stocked with fish from those unstocked (Gliwicz, 1967; Andersson, 1968; Grygierek, 1979). According to Kajak *et al.* (1976), the increasing density and biomass of small zooplankters not only result from a compensatory effect, but also from the general improvement in food availability for all zooplankters, as shown by the increasing size and fecundity of large disappearing, as well as, small crowding species.

Hillbright-Ilkowska *et al.* (1973) suggested that possible changes in the food composition of the fish fry species occurred at the highest fish stock. The stocking of older fishes (especially carps) increased the consumption of the two largest crustaceans (*Daphnia cucullata* and *Eudiaptomus graciloides*), and shifted, through competitive processes, the food preference of fry towards smaller prey species. Thus, *Diaphanosoma brachyurum*, although not susceptible to predation by old stocked fish, progressively disappeared from year to year.

2. Indirect effect on phytoplankton communities

The results presented in section III show that particulate feeders are 'active visibility-selective predators' on zooplankton and do not consume phytoplankton. But, apart from the well known shift in zooplankton populations towards smaller species, particulate feeders induce an increase in phytoplankton standing-crop and productivity. Hurlbert *et al.* (1972) observed that tiny blue-green unicells of *Coccochloris peniocystis* formed persistent algal blooms (at $200 \cdot 10^6$ cells per ml) in *Gambusia* pools, whereas in control pools (without *Gambusia*) this algae was absent and the water transparency improved. *Gambusia* feeding did not affect phytoplankters larger than $15 \mu\text{m}$ (such as *Pandorina*, *Pediastrum*, *Scenedesmus*, and *Haematococcus* species), but altered the cycling of

phosphorus by enhancing particulate phosphorus concentrations by an order of magnitude. Following the mechanistic interpretation of the zooplankton community dynamics of Pleasant Pond (Minnesota) on the basis of predation and competition considerations (Lynch, 1979), Lynch & Shapiro (1981) analyzed, through a combination of enclosure experiments, the differential role of grazing and nutrient enrichment on its phytoplankton community. They observed that in bluegill enclosures: (1) the large herbivores (*D. pulex*, *D. claviger*, and *C. reticulata*), which dominated both control enclosures (without fish) and the pond, were removed and replaced by smaller *B. longirostris* and rotifers, and (2) the total algal biomass (initially represented by flagellates *Cryptomonas marsonii*, *C. tetrapyrenoidosa*, and *Heterochromas globosa*, by desmids *Cosmarium* spp., *Closterium moniliferum*, and *Penium* sp., and by the dinoflagellate *Ceratium hirundinella*) increased over the control densities by more than an order of magnitude, because of the enhancement of other algal species (*Oocystis lacustris*, *Anabaena civerinalis*, *Aphanizomenon* sp.), mostly undetectable in absence of fish. Shapiro (in litt.) believes that Lynch (loc. cit.) misidentified the *Aphanizomenon* species: it probably was not *A. flos-aquae* which exists only as flakes.

Thus, the selective removal of zooplankton by visual predation of bluegill resulted, rather, in an alteration of the phytoplankton community, than in a simple enhancement of algal species. Simultaneously, the significant drop in soluble reactive (i.e., available) phosphorus concentration occurring in fish enclosures, suggests that phosphorus turnover rates may increase, following its regeneration by both fish and resulting dense populations of dominant small herbivores. Dense blooms of filamentous blue-greens persisted in enclosures with increasing fish predation pressures (*Anabaena circinalis*), or developed at the highest fish predation pressures (*Anabaena* sp.). These blooms were, nevertheless, different from the 'grass-blade' blooms occurring usually in the pond (only when the bottom waters were well oxygenated), as they consisted of various co-existing species of single filament colonies. As an exception, the gelatinous blue-green *Chroococcus dispersus* (the only species ungrazeable by large herbivores) decreased in the absence of large herbivores which were removed by bluegill, possibly by losing the nutritional advan-

tage from passing through herbivore guts. Lynch & Shapiro (loc. cit.) stressed that phosphorus and nitrogen enrichments have a rather distinct effect on phytoplankton. These enrichments may (1) shift algal species composition without increasing total algal biomass, and (2) increase primary productivity without affecting phytoplankton abundance or species composition (as previously observed by Losos & Hetesa, 1973).

Although decreases in phytoplankton biomass following zooplanktivore introductions have been reported, they correspond to particular situations (1) where uptake of nutrients by abundant macrophytes limit the phytoplankton response to zooplankton removal by fish (Hall *et al.*, 1970), or (2) where the bottom sediments of shallow water bodies are stirred up by the fish feeding activities, inhibiting phytoplankton photosynthesis through a decrease in light penetration (Grygierek, 1962, 1979; Spodniewska & Hillbricht-Ilkowska, 1973; Hillbricht-Ilkowska & Weglenska, 1973).

B. Impact of filter feeders

1. Direct effect on zooplankton communities

Contrasting with the relatively well documented impact of particulate feeders on plankton communities, little attention has been devoted to the impact of filter-feeding fishes. Almost nothing is known about the impact of tow-net filter feeders, whereas more information is available for pump filter feeders.

Pump filter feeders are 'passive escape-selective predators' on zooplankton plus 'passive size-selective grazers' on phytoplankton (see section III.B.2.), whereas particulate feeders are only 'active visibility selective predators' on zooplankton (see section III.A.1.). Thus, it might be expected that filter feeders (which have highest feeding rates, i.e., passive feeding selectivities for the most easily captured zooplankters, and feeding rates on phytoplankton increasing as (log) functions of particle size) have an effect on both phyto- and zooplankton community structures different from the effect of particulate feeders (which usually locate and preferentially attack zooplankters on the basis of their body visibility, and do not consume phytoplankton).

Pump filter-feeding gizzard shad reduce populations of *Keratella* sp., copepod nauplii, cyclopoid

copepodites, do not affect *Chaoborus* and *Diaphanosoma*, and enhance *Diaptomus pallidus* populations (Drenner *et al.*, 1982a; and reanalysis in Drenner *et al.*, 1984a) (see Fig. 13). In pond experiments, Drenner *et al.* (1984b) showed that the impact of pump filter-feeding blue tilapia, *T. aurea*, on the zooplankton community is somewhat similar to that observed for gizzard shad. The fish suppress the rotifer *Keratella* sp. (a weak swimmer), and enhance copepodid and adult stages of the large copepod *Diaptomus* sp. (the most evasive zooplankter in the pond). Thus, predation pressure by pump filter-feeding fish tends to shift the zooplankton communities towards the more evasive

zooplankters, such as calanoid copepods (for example, *Diaptomus* sp.). Nevertheless, this general trend may be altered by the fish filtering simultaneously and selectively on the phytoplanktonic food of the herbivorous zooplankton.

2. Direct effect on phytoplankton communities

In enclosure experiments carried out in the eutrophic pond Lake Warniak (Mazurian lakeland, Northern Poland), Kajak *et al.* (1975) looked at the potential use of omnivorous silver carp, *Hypoththalmichthys molitrix*, to overcome algae blooms and, thus, to improve water quality. Using replicated shallow plastic enclosures (1.5 m deep)

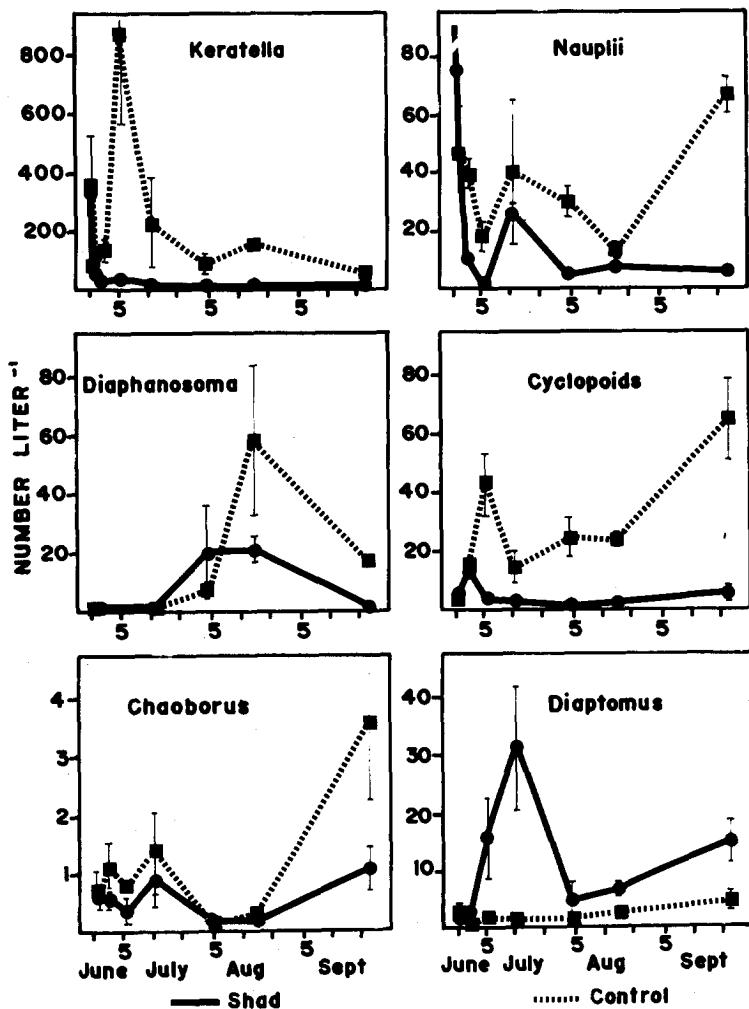


Fig. 13. Mean changes in densities of dominant zooplankton in replicate ponds containing gizzard shad (*Dorosoma cepedianum*) and control ponds without fish. The bars represent the range of observed densities (Drenner *et al.*, 1982a).

opened to the sediment, with no fish (control), moderate and high fish densities (respectively, 450 and 1350 kg per ha), the authors demonstrated that silver carp reduced by 4.5 times the average biomass of phytoplankton, regardless to fish density (and 16 times the biomass of zooplankton at the highest fish density). Higher fish densities reduced blue-green algae and enhanced dinoflagellates and nannophytoplankton. Moreover, in the gut contents of the fish kept permanently on natural food in net cages, *Microcystis aeruginosa* was dominant (together with some crustaceans and rotifers).

Kajak *et al.* (loc. cit.), Kajak (1977), and then Kajak *et al.* (1977), comparing the feeding of silver carp in eutrophic lakes of various plankton composition and biomass, emphasized that the fish impact may differ according to the environmental conditions. First, the elimination of the consumed seston from the water column by the way of feces sedimentation may have contributed to the depletion of plankton and to the enrichment of benthos (especially Oligochaeta). This falling down of substances to the bottom, certainly advantageous for the purity of water, is more likely to occur in stratified water bodies where long-term isolation of substances from the circulation in the epilimnion may take place. But, it would probably not happen in (frequently or permanently) well-mixed aquatic systems, or in shallow habitats in presence of intensive mixing of bottom sediment by benthophagous fish. Second, silver carp is able to feed on bottom sediments, allowing its successful survival during periods of low plankton biomass and its sufficient abundance to meet and overcome developing algae blooms. But silver carp cannot digest the ingested cells of filamentous blue-green algae (larger trichomes 300–500 µm in length and 6 µm in diameter of *Oscillatoria agardhii*, and colonial forms of *Aphanizomenon flos-aquae*), whereas *Ceratium hirundinella* and diatoms are well digested. Blue-green algae are consumed only when abundant. Even, in some cases, silver carp avoid blue-green algae (Omarov & Lazareva, 1974; Vovk, 1974). When blue-green algae are dominant the fish stop feeding (Savina, 1965; after Vovk, loc. cit.), its growth rate slows down (Omarov & Lazareva, loc. cit.), and spitting out of food may occur (Savina, loc. cit.). In addition, silver carp suffer high mortality rates during periods of mass 'water-blooms' of filamentous blue-green algae when kept in net cages without

any access to the bottom food sources. Third, the indirect effect of silver carp on phytoplankton through the consumption of filter-feeding zooplankton seems to be even more important than its direct grazing effect. Actually, the grazing pressure of herbivorous zooplankters on nannophytoplankton decreases whereas fish grazing on net-phytoplankton shifts the competitive balance in favour of smaller phytoplanktonic forms, as well as, modifies the dynamic of physical and chemical factors.

Thus, filter-feeding silver carp favour nannophytoplankton against netphytoplankton, as not only its competitor (netphytoplankton) is removed, but also its consumer (filter-feeding zooplankton), as confirmed by Kajak *et al.* (1975)'s results. Kajak *et al.* (1977) suggested another mechanism which may play a role in the enhancement of nannophytoplankton. Although data on silver carp feeding selectivity on zooplankton are lacking, the authors expected that predatory cyclopoids can avoid the capture by the filtering fish. Thus, by increasing the predation pressure upon the filtering zooplankton and leaving their predators, silver carp would decrease the invertebrate grazing pressure, and consequently enhance nannophytoplankton.

Nevertheless, Januszko (1974) found that, in ponds, generally netphytoplankton and particularly diatoms were stimulated by silver carp, whereas nannophytoplankton was inhibited. Since the fish does not feed on nannophytoplankton, selecting only particles larger than 20 µm (Boruckij, 1973), Kajak *et al.* (1975) stated that the observed decrease of nannophytoplankton abundance resulted well from the transformation of the environment by fish, but not from grazing. Such transformations have been shown in experiments where the proportion of nannophytoplankton increased but its absolute biomass strongly decreased.

In pond experiments with two replicates, Drenner *et al.* (1984b) showed that blue tilapia suppressed significantly populations of the largest *Urogljenopsis* (500 µm) and *Ceratium* (180×150 µm) algal species. *Oocystis* (25×15 µm) and *Navicula* (60×30 µm), though of appropriate dimensions to be consumed efficiently, were not suppressed probably because smaller algae have generally higher growth rates (Banse, 1976; Schlesinger *et al.*, 1981; Smith & Kalff, 1982). The smallest

Rhodomonas ($8 \times 5 \mu\text{m}$), *Chrysochromulina* ($6 \times 5 \mu\text{m}$), *Chlamydomonas* ($5 \mu\text{m}$), and *Cyclotella* ($6 \times 3 \mu\text{m}$) species were enhanced in the presence of fish, possibly due to inefficient filtration, nutrient regeneration by fish, nutritional advantage from passing through herbivores gut, higher growth rates, or modification of herbivorous zooplankters community.

Drenner *et al.* (1984a), using similar field approaches, showed that omnivorous filter-feeding gizzard shad only significantly suppressed *Ceratium* ($170 \times 48 \times 30 \mu\text{m}$). They did not significantly affect populations of *Synedra* ($170 \times 1 \mu\text{m}$), *Peridinium* ($20 \times 24 \mu\text{m}$), *Navicula* ($16 \times 3 \mu\text{m}$), *Kirchneriella* ($8 \times 1.5 \mu\text{m}$), *Cyclotella* ($6 \times 3 \mu\text{m}$), and *Chlamydomonas* ($5 \mu\text{m}$), but enhanced populations of *Ankistrodesmus* ($20 \times 1 \mu\text{m}$), *Cryptomonas* ($16 \times 6 \mu\text{m}$), *Cosmarium* ($10 \times 1 \mu\text{m}$), *Rhodomonas* ($6 \times 4 \mu\text{m}$), and $2-4 \mu\text{m}$ algae and bacteria.

Thus, filter-feeding fish have a different effect on plankton community than visual particulate-feeding fish. However, the enhancement of nanophytoplankton by filter-feeding gizzard shad and blue tilapia looks similar to that observed in presence of visual feeding fish (Andersson *et al.*, 1978; Hurlbert & Mulla, 1981; Lynch & Shapiro, 1981), probably as a response to pond nutrient levels (not monitored), fish digestive activities, and zooplankton suppression.

Filter-feeding fishes are 'passive size-selective grazers' but, their direct grazing impact on phytoplankton is a consequence of the relation between fish feeding rates and algal growth rates. The latter usually decreases with increasing algal size. As filter-feeding shad and tilapia have the highest feeding rates for the larger slow growing algae, they have the potential to suppress directly the larger phytoplankters such as *Ceratium*.

VII. Conclusions: Biomanipulation approaches for lake management and needs for future research

In summary, the Holling's approach is extended in this review from particulate feeders to filter feeders so as, for each planktivore type and in various environmental conditions, to (1) determine the relative importance of the different factors responsible for the planktivore selectivity, (2) outline qualitative mechanisms of functional or adaptative rela-

tionships between the planktivores and their planktonic foods, and (3) discuss respective potential vulnerabilities of various plankter types to foraging activities of planktivores.

The information presented here is expected to be appropriate and helpful in documenting fish/plankton interactions, discerning mechanisms of selective (or random) prey collection by planktivorous fishes, and elucidating observed changes in plankton community structures. It is obvious that laboratory experiments, coupled with complementary field data analysis, are indispensable for meaningful tests of proposed mechanisms and accurate predictions of community responses to fish predation pressures.

Since, in addition to competition for food and nutrient limitation, predation is generally recognized as an important driving force structuring communities in freshwater systems, the structure of limnetic plankton communities can be predicted from the knowledge of the types and the importance of the predators present (Zaret, 1980). The level of predation pressure and the nature of the planktivorous fishes may well predict the respective vulnerabilities of the different available planktonic prey species. These predictions (see section V. on models) can be used to study meaningfully the potential impacts of the concerned planktivores on plankton communities.

Experimental studies investigating the mechanisms of ecosystem trophic level alteration by planktivorous fishes have been scarce. Hurlbert & Mulla (1981), summarizing the effects of fish introduction (or removal) presented in the literature, emphasized that many studies (including those of Hrbáček *et al.*, 1961; Brooks & Dodson, 1965; Straškraba, 1967; Wells, 1970; Hutchinson, 1971; Hillbricht-Ilkowska & Weglenska, 1973; and Andersson *et al.*, 1978) have been done only in a rather descriptive or quasi-experimental manner, usually lacking controls or replications. Hurlbert & Mulla (loc. cit.) noticed that the few really experimental studies (among which are those of Grygierek, 1962; Grygierek *et al.*, 1966; Hall *et al.*, 1970; Hurlbert *et al.*, 1972; Losos & Hetesa, 1973; Lynch, 1979; and their own study on *Gambusia affinis*) have not been designed to allow successful application of inferential statistics.

It also appears that even knowledge coming from well designed experimental field studies in con-

trolled environments (such as tanks, experimental ponds, or 'in situ' plastic suspended enclosures) may not be working properly for understanding the functioning of natural environments if the feeding mechanics of the experienced fish are unknown. If laboratory measurements concerning feeding behaviours, selectivities and rates are lacking, it is difficult to separate direct from indirect effects of fish predation. Dynamic views considering the community modifications as a combination of direct consequences of the fish predation plus indirect, often dominant, consequences of resulting trophic level interactions are prevalent concepts among the more recent studies. The current tendency is to use three complementary interactive approaches: laboratory experiments of fish feeding mechanics, field tests of plankton community responses to fish predation, and ecological models of trophic state modifications of lakes based on fish/plankton interactions. The laboratory feeding trials determine the feeding behaviours, selectivities and rates of the fish, and serve to build the predation model. Then, the model is used to generate predicted alterations of the aquatic ecosystem which are statistically compared with alterations observed during field experiments (Wright & O'Brien, 1984; Drenner *et al.*, 1984a). The discrepancy between the observed and the predicted alterations permits one to discern the actual mechanisms involved and to produce new ideas to be tested. These are basic goals in ecology.

Lynch & Shapiro (1981) addressed the planktivorous fish from the community standpoint. They emphasized that the response of a lake to enrichment not only depends on its initial nutrient capacity, but also on the structure and density of its planktivorous fish community. They suggested that in lakes with planktivorous fishes, the phytoplankton community may respond more dramatically to enrichment than in lakes free of planktivores where algae are maintained in critical nutrient availability situations. From the limnological viewpoint this has considerable consequence, and implies that not only trophic conditions of lakes are somewhat related to the presence of planktivorous fishes (Hrbáček, 1969), but besides, that the 'ecological buffer capacity' of lakes (term defined by Jørgensen & Mejer, 1977) may be lowered at higher planktivore predation pressures.

Using enclosures, Andersson *et al.* (1978) studied the indirect effect of planktivorous and ben-

thivorous fish on both phytoplankton and physico-chemical water conditions of eutrophic Swedish Lakes Trummen and Bysjön. The authors observed that in fish enclosures (stocked with bream, *Abramis brama*, and roach, *Rutilus rutilus*, in Lake Trummen, and only with crucian carp, *Carassius carassius*, in Lake Bysjön) water turbidity increased, blue-greens *Microcystis* spp. developed blooms (whereas phytoplankton populations at the beginning of the experiment consisted of cryptomonads, small blue-greens, and diatoms), and pH became more basic. As previously shown by Lamarra (1975), Hrbáček *et al.* (1978) and Nakashima & Leggett (1980) fish may contribute to the nutrient budget of lakes because of their digestive activities, but the importance of this process remains still debatable (see Shapiro & Carlson, 1982, and Nakashima & Leggett, 1982). Hurlbert *et al.* (1972) remarked that, although in nature, *Gambusia* and other zooplanktivores are limited by the predation of piscivores, in some cases the man-caused alterations in fish populations (rather than man-caused increases in nutrient inputs) may result in the eutrophication symptom of excessive algal growth. Their idea coincides with Shapiro *et al.*'s (1975) suggestion to use the artificial increase of piscivore populations as a potential biological control of phytoplankton levels (unless undesirable enhancements of filamentous algae and higher plants have occurred), and emphasized that fish ought to play a more important role in the restoration approaches of eutrophicated water bodies.

In a more recent study conducted in man-made ponds with adequate controls and replications, Hurlbert & Mulla (1981) examined in detail the community effects of *Gambusia* predation, and particularly its most conspicuous effect of increasing phytoplankton biomass. Andersson *et al.* (1978) and Hurlbert & Mulla (1981) increased the credibility of Shapiro *et al.*'s (loc. cit.) suggestion of planktivorous fish biomanipulation as a potential method for reducing phytoplankton densities.

Numerous studies demonstrated that a reduction in fish populations resulted in an evolution of the pelagic zone towards oligotrophic conditions (Hrbáček *et al.*, 1961; Novotna & Korinek, 1966; Losos & Hetesa, 1973; Andersson *et al.*, 1978; Stenson *et al.*, 1978; Weglenska *et al.*, 1979; Cronberg, 1980; Leah *et al.*, 1980; Stenson, 1982, 1983; Reinertsen & Langeland, 1982; Langeland &

Reinertsen, 1982; Olrik *et al.*, 1984; Reinertsen & Olsen, 1984). Andersson *et al.* (1978) tested, on a large scale, the biomanipulation approach of controlling trophic states. Extensive experimental removals of planktivores, and simultaneous releases of piscivorous fishes were realized in Lake Trummen. Although the zooplankton was not significantly affected either in composition or in abundance, the total phytoplankton biomass, total P and total N, decreased moderately. However, Andersson *et al.* (loc. cit.) concluded that, not only do fish directly affect the biomass of their prey, but they also have an indirect influence on trophic level interrelationships, mineralization processes, and nutrient availability.

A rather extensive literature is devoted at present to the feasibility of biomanipulation approaches to restore lakes and reservoirs (e.g. Shapiro, 1978, 1979; and Leventer, 1981). Thanks to the increasing knowledge of the role of community interactions in eutrophication processes, besides classical restoration procedures involving almost exclusively engineering techniques, we now have an alternative approach (in order to avoid high economic associated costs and/or common irrelevance of more conventional approaches) consisting of more subtle ecological shiftings of trophic state balances.

To check the importance of biotic feedback interactions in the trophic properties of lake, Henrikson *et al.* (1980) removed fish population (by means of rotenone) from a Swedish lake. Roach (*Rutilus rutilus*) elimination resulted in oligotrophication symptoms, such as: (1) a shift of predominant small cladocerans (*Bosmina longirostris*) towards larger copepods (*Eudiaptomus gracilis*), (2) an increase of net-phytoplankton biomass where dominant *Peridinium aciculiferum* (30 µm) were replaced by *Ceratium hirundinella* (300 µm), (3) a decrease in nannoplankton abundance followed by an increase in transparency, (4) a dramatic 90% lowering of limnetic primary production, and (5) a decline in pH, total P and total N.

In order to reduce the abundance of algae in Round Lake (a small urban lake in Minnesota), Shapiro & Wright (1984) tested the applicability of the biomanipulation approach, using rotenone to eliminate planktivorous and benthivorous fish. Over a two-year period following this manipulation they observed a shift towards less eutrophic conditions, such as: (1) a significant increase in secchi

disk transparency (2.1 m and 4.8–6.0 m, before and after, respectively), (2) a marked decrease in chlorophyll *a* concentrations (up to 12 µg l⁻¹, and less than 5 µg l⁻¹, before and after, respectively) associated with a change in algae composition (from dominance by various Chlorophyceae species to dominance of *Cryptomonas erosa*) and a decrease in algae densities, (3) a change in herbivorous crustacean community (from small-bodied *Bosmina longirostris*, *Ceriodaphnia reticulata*, and *Daphnia ambigua* to large-bodied *D. parvula*, *D. galeata mendotae*, and dominant *D. pulex*) associated with a decrease in abundance and a considerable increase in mean size of herbivorous zooplankters, and (4) a decrease in epilimnetic concentrations of total P (and, to a lesser extent, total N). Additional bioassay experiments showed that the grazing pressure imposed by the resulting herbivorous *Daphnia* populations (mainly *D. pulex* and *D. galeata mendotae*) was able to keep low chlorophyll concentrations and algal abundances, even at high inorganic N and P concentrations. This suggested that the oligotrophication symptoms resulted only from the changes in herbivore populations. Shapiro & Wright (loc. cit.) calculated that the biomanipulation increased two to three times the grazing pressure responsible for the reduced chlorophyll and nutrient concentrations. Nutrient depletion accompanying a shift in herbivorous zooplankton from small-bodied *Bosmina/Ceriodaphnia* to large-bodied *Daphnia* community was also observed by Stenson *et al.* (1978) and Shapiro *et al.* (1982).

Wright & Shapiro (1984) supported that, by migrating daily, *Daphnia* actively transport nutrients downward out of the epilimnion. The authors suggested that biomanipulation could alter the importance of the nutrient depletion in the epilimnion by changing the migratory patterns of the zooplankton community. However, the absence of replicates in the experimentations of Henrikson *et al.* (loc. cit.) and Shapiro & Wright (loc. cit.), and, to a lesser extent of controls, prevented any rigorous statistical interpretation of the observed oligotrophication symptoms resulting from fish population elimination. It was not possible to test the contributions of annual variations in nutrient loading and climatic conditions. Moreover, rotenone emulsives in concentrations commonly used to eradicate fish populations (0.5–0.6 ppm.) are

known to be strong enough to kill most zooplankters in a few hours (most species of rotifers: *Keratella*, *Trichocerca*, *Asplanchna*, *Synchaeta*, *Polyarthra*, *Filinia*; copepods: *Diaptomus*, *Eurytemora*, *Cyclops*; and highly vulnerable cladocerans: *Daphniosoma*, *Daphnia*, *Ceriodaphnia*, *Bosmina*), and also some phytoplankters (such as *Ceratium hirundinella*) (Almquist, 1959). Although less sensitive than fishes, benthic invertebrates are vulnerable to rotenone concentrations above 0.5 ppm (Lindgren, 1960): for example, all instars of *Chironomus* sp. were exterminated by a long term effect of rotenone treatment (Koksvik & Aagaard, 1984). As Round Lake was newly stocked with planktivorous, piscivorous, and benthivorous fish, the effects of biomanipulation only persisted for two years, whereas they lasted for at least four years in a lake kept free of fish (Henrikson *et al.*, loc. cit.). The limited duration effects of a single biomanipulation treatment support that (1) biomanipulation must be combined with more traditional approaches, and (2) long-term beneficial effects could be maintained only through successive implementations of adjusted biomanipulation treatments, in order to sustain the best desirable trophic improvements.

However, biomanipulations is not yet a science, as not all interactions may be always under control: but it is still experimental. Two examples may be used to show the hardness to control some indirect effects of predation by visual planktivores on filter-feeding crustacean zooplankton and phytoplankton communities: (1) resulting dominant populations of large *Daphnia* may be unable to regulate the growth rate of such an alga as *Aphanizomenon* spp. (not readily grazable by large herbivorous zooplankters) which may efficiently use the nutrients available of lakes (Shapiro, 1978), and (2) visual planktivorous fishes may indirectly influence the zooplankton grazing pressure and thus the algal growth, if they selectively remove carnivorous zooplankters, such as chaoborids (Stenson, 1972, 1978, 1980; Northcote *et al.*, 1978) and cladocerans *Leptodora* and *Bythotrephes* species (De Bernardi & Giussani, 1975), which are efficient predators on *Daphnia*.

As the selective (often differential) impacts of various species of planktivorous fishes are now well documented, a main motivation in limnology ought to consider the planktivore influence from

the community point of view. Planktivorous fish communities usually comprise both particulate feeders and filter feeders, but it always remains unknown how the differential effects of these planktivores combine between them to structure plankton communities.

Filter-feeding fishes have the potential advantage over visual planktivores, to consume selectively net-phytoplankton, to create situations in which nanno-phytoplankton is favoured, and thus to induce better water quality levels. But, environmental conditions affecting decomposition processes and nutrients regeneration, such as water temperature, mixing pattern, residence time, surface level fluctuation, and initial trophic state, must play a decisive role in obscuring the beneficial impact of filter-feeding planktivores. Tests of the potential ability of filter-feeding planktivores to control algae blooming are still dramatically lacking over a wide range of environmental conditions. For example, it might be expected that in tropical aquatic environments, due to higher water temperatures, the pressure of filter-feeding planktivores on the whole ecosystem could be even higher at much lower fish densities, than in temperate zones where filter feeding is generally less important (even occasionally lacking) than particulate feeding, and where large herbivorous zooplankters account for most of the grazing pressure on algae. Much attention ought to be paid to filter-feeding planktivorous fishes (and particularly in the tropics; for example, see Nilssen, 1984) for their potential for biological control of net-phytoplankton. Special interest might be dedicated to the control of undesirable filamentous, usually toxic, algae, through direct fish grazing or indirect enhancement of grazing by large efficient herbivorous zooplankters (such as, *Daphnia pulex*; see Lynch, 1980; Holm *et al.*, 1983; Carlson & Schoenberg, 1983). Looking at natural and man-modified balances between dominant visual planktivore communities (i.e., particulate feeders), and dominant filter-feeding planktivore communities, in lakes and reservoirs of various trophic states, latitudes (effect of temperature), mixing patterns, residence times, and surface level fluctuations, may give interesting insights for understanding and controlling eutrophication.

Information on fish feeding ecology based only on stomach content analyses readily discerns the trophic levels of the fish food, but it is insufficient

to quantify its utilization. The mechanisms governing fish feeding selectivity and resource use are not always well understood. More studies are needed to identify dominant mechanisms and to predict long-term changes in plankton communities exposed to fish predation. Combined laboratory experiments, field tests and simulation models will give profitable insights. To reach the goal of considering planktivore influence as multi-level effects coupled with interactive community responses, it appears important to document some strategic mechanisms, such as (1) the indirect response of phytoplankton to the selective depletion of zooplankton by particulate feeders, (2) the differential utilization of phytoplankton, detritus, and suspended organic particles by pump and tow-net filter feeders, (3) the selective removal of zooplankton by pump and tow-net filter feeders, (4) the contribution of planktivorous fish feeding activity in the nutrient loadings and dynamics of lake ecosystems, and (5) the digestion efficiencies of filter-feeders for algae (especially large undesirable species). Obviously, predation pressures by other trophic levels (piscivores, non-piscine vertebrate planktivores, invertebrate planktivores), as well as, mineralization processes, external nutrient loadings, and competition for food sources, must not be neglected. More information on the driving forces governing the structure and dynamic of freshwater communities is urgently needed to understand better the functioning of limnological ecosystems, and to make good decisions in the field of lake and reservoir management.

Exotic fish introduction are clear examples of this critical necessity (see Gophen *et al.*, 1983a, 1983b). General information on the role played by fish populations in the eutrophication process are lacking. More studies should be devoted particularly to the interactions between trophic state modifications and changes in the fish community. Stressing that relatively few works document the effects of the fish fauna on the eutrophication processes compared to the numerous ones illustrating the effects of eutrophication on the fish community and production, Opuszyński (1979b) studied the interactions between fish stock compositions and eutrophication processes, using increasing densities of common carp and silver carp, alone or combined, in experimental ponds. He developed the 'ichthyoeutrophication concept' which assumes that

changes in the water environment induced by nutrient enrichments generate changes in the fish community, which in turn generate additional changes in the water environment. Applying this concept, Opuszyński (*loc. cit.*, 1980) showed that the introduction of single species of fish to counteract eutrophication appears erroneous. He suggested that fishery management approaches used against eutrophication processes should try to maintain the original ichthyofauna structure (in order to increase the precision of the self regulating capability of the system), instead of introducing species improving the fishery production. Such a concept remains to be tested.

Aquatic ecosystems functioning could be better understood if considered from the point of view of optimized community interactions versus environmental condition changes (temperature, mixing pattern, residence time, surface level fluctuation, and trophic state). Nevertheless, predation by planktivorous fishes is not always the main determinant responsible for the changes in plankton communities (for example, see Gliwicz & Prejs, 1977). As concluded by Zaret (1980), it is essential to identify what circumstances make predation, rather than competition or nutrient limitation, to become the dominant structuring force.

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