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Food composition and zooplankton selection by smelts, *Osmerus eperlanus* L., in Lake Tyrifjorden, Norway

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Stomach analyses were carried out on 80—160 mm long smelts sampled monthly from May 1976 to September 1977. The amount of food was lower from February to April than during the rest of the year. Zooplankton dominated the smelts' food from July to February, while zoobenthic insect larvae and nymphs were more important from March to June. Cladocerans were prefered to copepods during most of the year. From July to April cladocerans made up from 30 to 95 % of the diet, while 10 to 60 % of the smelts' food in spring and summer consisted of copepods. Benthic copepods occurred in the stomachs almost troughout the year. *Daphnia galeata* and *Bosmina longispina* were the most important species in the smelts' diet and they were positively selected, together with *Leptodora kindti, Bythotrephes longimanus* and *Heterocope appendiculata.* The most common copepods in the zooplankton, *Eudiaptomus gracilis,* was negatively selected by the smelts.

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INTRODUCTION

Smelts *(Osmerus* spp, Osmeridae) play an important part in many lakes' food chain, both as a dominating predator on zooplankton and as prey for salmonids, perch *(Perca fluviatilis)* and zander *(Stizostedion lucioperca)* (Cooper 1940, Svärdson 1976). Besides zooplankton, smelts feed on benthic animals (Nordquist 1910, Willer 1926, Leskien 1942) and the food habits may thus vary between populations (Belyanina 1969, Rembiszewski 1970). Seasonal changes within the same population do also occur (Czeczuga 1959, Bergaust 1972, Hakkari 1978). Smelts have nocturnal vertical migrations towards the surface during summer and autumn (Anderson 1968, Northcote and Rundberg 1970, Dembinski 1971). The up- and downward migrations occur in a three hour period at dusk and dawn. During these migrations smelts move into water layers richer in zooplankton, where they feed. In winter and spring the vertical migrations are discontinued as a result of low temperatures and low density of plankton in the upper water layers (Dembinski op.cit.)

Studies of planktivorous fish species have also documented selection of zooplankton species (Brooks and Dodson 1965, Galbraith 1967, Bernardi and Giussani 1975). The purpose of the present investigation was to study the food composition of smelts through the year in lake Tyrifjorden and to discover whether the smelts were selecting any of the zooplankton species in the plankton community.

Lake Tyrifjorden lies in the southeastern part of Norway (59°53'-60°8'N, 10°-10°21'E). The lake has a surface area of 134,1 km^2 and lies at an altitude of 64 m. Maximum depth recorded is 295 m and mean depth 114 m. The limnology of the lake has been well documented by several authors (Strøm 1932, Nyhagen 1959, Holtan 1970). During summer the metalimnion occurs at a depth of 15—20 m, and temperature in the epilimnion varies between 8 and 17°C. There is little variation in pH, which is around 7.0. The ecological condition of the lake may be interpreted as incipient eutrophication (Langeland 1974). Twelve fish species have been recorded from the lake (Langeland 1971).

MATERIAL AND METHODS

Smelt adults ranging from 80—160 mm total length were captured with gill nets of mesh size 10 mm. The smelts were sampled monthly, except January, from May 1976 to September 1977. The vertical distribution of smelts in Tyrifjorden during the winter was not studied, but the smelts probably stayed near the bottom as a result of low water temperatures (c.f. Dembinski 1971). In summer 1976 nocturnal migrations of

Table 1. Mean dry weights of different food items of smelts in Tyrifjorden from May 1976 to September 1977.

Food items	No of animals	Dry weight microgram	Size mm
Daphnia galeata	44	16.3	1.4 - 1.6
Bosmina longispina	38	9.0	0.7 - 0.8
Leptodora kindti	15	96.0	5.0 - 7.0
Bythotrephes longimanus	7	35.1	1.6 - 1.8
Holopedium gibberum	18	27.3	1.2 - 1.3
Heterocope appendiculata	29	38.9	1.9 - 2.1
Limnocalanus macrurus	19	22.7	2.2 - 2.3
Eudiaptomus gracilis	23	8.7	1.2 - 1.3
Cyclops spp.	30	9.1	1.3 - 1.5
Megacyclops gigas	14	90.4	2.8 - 3.1
Eucyclops serrulatus	20	10.4	1.3 - 1.4
Harpacticoida	34	5.1	0.8 - 0.9
Chironomidae larvae	15	430	6.0 - 8.0
Ceratopogonidae larvae	18	160	6.0 - 8.0
Ephemeroptera nymphs	8	1700	9.0 -11.0
Trichoptera larvae	7	1700	9.0 -11.0

the smelts were observed with echo sounder. The smelts stayed near the bottom at depths from 15—25 m during daytime. At night they migrated towards the surface and returned to the bottom at dawn. When studying seasonal changes in food of fish, it is important that the stomach samples are collected with the same method and thus are comparable. It was presumed that nets placed near the bottom at depths from 15—25 m at dusk and pulled 2—3 hours after dawn, constituted the best method for capturing smelts through the year in Tyrifjorden. In summer and autumn this method captured smelt at the end of the nocturnal migration cycle.

During the spawning run in May about 80 % of the smelt stomachs were empty (Garnås 1978). The data from this month are therefore based on smelts captured after the spawning. The stomachs were preserved in 10 % formalin immediately after capture and between 30 and 100 stomachs were examined each month. The insects were identified to order or family and the crustaceans to species or generic group.

To express the relative importance of each food category, a combination of numerical and gravimetric methods was used (Hynes 1950, Hyslop 1980). The food items in each stomach were counted and the most common body size of the food items was measured. Dry weights of non-consumed specimens of the same size were determined after drying at 60°C (Edmondson 1971, Man and Hodgkiss 1977) (Tab. 1). The specimens used for dry weight determinations were collected at different times of the year, to allow seasonal changes in weight as observed for chironomids (Jonasson 1972).

Zooplankton was sampled monthly at the same time and from the same areas as the smelt samples, using a net with net opening 29 cm and mesh size 90 µm. Three vertical hauls from 25 m to the surface were collected each month,

Table 2. Mean number of zooplankton in Tyrifjorden in 1976 and 1977, based on three vertical net hauls.

	1976								1977							
	M	J	J	A	S	O	N	D	F	M	A	M	J	J	A	S
Daphnia galeata	3	17	21	142	244	338	73	122	3	0,3		3	20	2	36	331
Bosmina longispina	75	122	83	207	221	330	101	99	12	8	9	56	116	50	215	164
Leptodora kindti				2	16	1	2	0.7							7	7
Bythotrephes longimanus			0.7	2										0.3		
Cyclops scutifer	111	175	29	10	5	7	2	13	18	4	4	116	167	30	9	4
Mesocyclops leucarti	5	4	7	77	32	17	1	0.3					4	8	15	11
Eudiaptomus gracilis	19	102	79	139	99	145	34	112	62	27	27	7	104	32	239	194
Heterocope appendiculata			12	139	3	3								0.3	46	6
Limnocalanus macrurus	7	3	1			0.7		0.3	0.3		2	88	193	110	9	8
SUM	220	423	233	718	620	842	213	347	95	39	42	270	604	232	576	725

sampling a total water volume of 3.7 liters. The adult specimens in each sample were counted and the mean number of each species per net haul was estimated (Tab. 2). The selectivity index of Ivlev (1961) was used to discover if the smelts selected certain crustacean species as food. Values obtained by this method range between -1 and $+1$. Negative values indicate selection against an item, and positive values indicate selection for an item. The formula for determining selectivity is:

$$E = (r_i - P_i) / (r_i + P_i)$$

where r_i is the percentage of an item in the stomachs and P_i is the percentage of the item in the environment.

RESULTS

Food composition

The mean weight of food per smelt stomach varied between 2.1 and 3.9 mg from June to August, except for August 1976 (Tab. 3). There were no significant differences in the weight of stomach contents in these months ($p > 0.05$). In September the amount of food dropped to 1.5 mg both years. From October to December the mean weight of food consumed varied between 2.1 and 3.1 mg. The lowest amount of food was calculated in winter from February to April. The dry weights of food ingested in these months were significantly lower than from June to August and from October to December ($p < 0.05$).

Table 3. Mean dry weight per stomach (mg) of food of smelts in lake Tyrifjorden in 1976 and 1977.

			1976						1977							
Month	M	J	J	A	S	O	N	D	F	M	A	M	J	J	A	S
Zooplankton	1.29	1.71	2.55	5.93	1.52	3.08	2.08	1.81	0.32	0.50	0.34	0.54	1.15	1.88	1.95	1.48
Zoobenthos	3.0	2.17	1.25	0.97	0.04	0.06	0.08	0.25	0.12	0.62	0.24	0.87	1.95	0.63	0.17	0.05
Sum	4.29	3.88	3.80	6.90	1.56	3.14	2.16	2.06	0.44	1.12	0.58	1.41	3.10	2.51	2.12	1.53
Standard deviation	5.81	3.96	3.08	5.60	1.59	2.66	1.40	0.99	0.82	2.46	0.99	3.05	2.58	1.82	1.56	1.08
No of fish examined	46	44	50	53	49	44	34	35	95	90	93	30	55	66	64	55

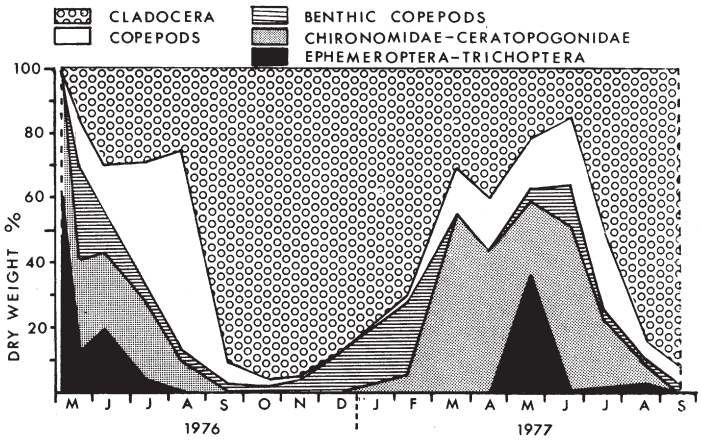

Fig. 1. Seasonal changes of different food categories of smelts in Tyrifjorden in 1976 and 1977, expressed as percent dry weight per fish stomach.

In the periods from May to September which were studied both in 1976 and 1977, there were no significant differences in mean stomach weights in June, July, and September ($p > 0.05$) In May and August the mean amount of food was significantly higher in 1976 than in 1977 ($p < 0.05$).

The frequencies of zooplankton varied from 85 to 100% in the stomachs during the sampling period except in May, and the mean dry weights were higher than the weights of zoobenthos through the year except in March, May, and June (Tab. 3). However zoobenthos occurred in more than 50% of the smelt stomachs mainly from December to August. Fish were not important as food for the smelts and were only observed in 2% of the stomachs in August and September. The fish which were eaten, were yearlings of smelt.

Cladocerans were more important as food than copepods during most of the year (Fig. 1). They had maximum occurrence from September to February, but occurred in 70 to 100% of the stomachs through the year except in May. Copepods were most important as food in spring and summer. In August 1976 they made up 60% of the stomach contents.

Benthic copepods (i.e. *Megacyclops gigas, Eucyclops serrulatus* and Harpacticoida) occurred in the stomachs almost through the year, but were most important from November to February and in May 1976. Larvae of Chironomidae and Ceratopogonidae were eaten by the smelts from February to August. From March to July these prey items occurred in 40 to 90% of the stomachs. Nymphs of Ephemeroptera and larvae of Trichoptera were ingested in May and June and occurred in 25 to 45% of the stomachs.

Zooplankton selection

Fig. 2 shows seasonal abundance of crustaceans in the zooplankton and in the stomachs of the smelts. *Daphnia galeata* had maximum occurrence in Tyrifjorden from August to December. However except in May, June, and July 1976, it was positively selected through the sampling period (Fig. 3). From February to May 1977 the selectivity index varied between $+0.82$ and $+0.89$. *Bosmina longispina* was abundant in the zooplankton during most of the year, but was only slightly selected by the smelts ($E < +0.48$). In August and September 1976 the smelts avoided *B. longispina* ($E = -0.98$ and -0.27). The large cladocerans *Leptodora kindti* and *Bythotrephes longimanus* were positively selected by the smelts when they occurred in Tyrifjorden from June to November ($+0.16 < E < +0.73$).

As for the copepods, *Heterocope appendiculata* and *Cyclops* spp. were positively selected by the smelts from July to September, and March to July respectively. Except in November and August 1977 the selectivity index of *H. appendiculata* varied from $+0.42$ to $+0.85$, and for *Cyclops* spp. from $+0.10$ to $+0.53$. From August to February *Cylops* spp were negatively selected ($-0.25 < E < -0.99$). The most frequent copepod in Tyrifjorden during the year was *Eudiaptomus gracilis*. However it was only observed in the smelt stomachs from March to May, and the copepod was therefore negatively selected by the smelts through the year ($-0.36 < E < -1.0$). *Limnocalanus macrurus* were numerous in the zooplankton from May to July 1977, but were not eaten by the smelts except in March.

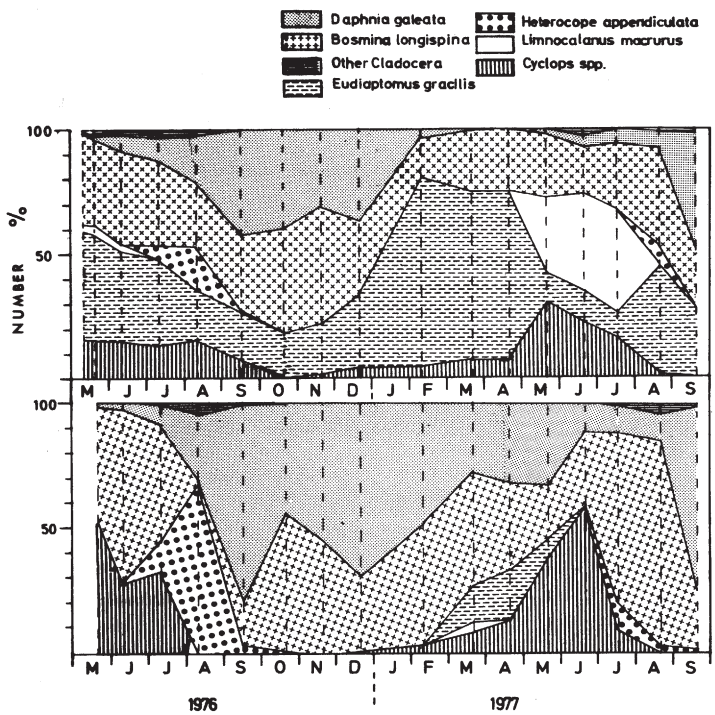

Fig. 2. Distribution of zooplankton species as percent of number in the plankton community (above) and in the smelt stomach (below) in Tyrifjorden in 1976 and 1977.

DISCUSSION

The results from Tyrifjorden indicated that zooplankton is the main food for the smelts during most of the year. Zooplankton has usually been reported to dominate the smelts' food in deep lakes (Milbrink 1973, Sandlund et al. 1980), while zoobenthos is of greater dietary importance in shallow lakes (Burbidge 1969, Bergaust 1972, Hakkri 1978). However zoobenthos occurred together with zooplankton in most of the stomachs from December to August, and was especially important in winter and spring in Tyrifjorden which is a deep lake. This may be a result of the sampling method. Because the smelts were captured with net along the bottom, the probability for catching smelts which had ingested benthos was higher than if sampling had been carried out in different water layers. But a mixed diet of zooplankton and zoobenthos may also be a result of vertical migrations. At night the smelts migrate towards the surface and feed on zooplankton, while zoobenthos is eaten when the smelts stay near the bottom during daytime. In winter and spring when the abundance of preferred zooplankton and water temperatures are low (Garnås 1978), the vertical migrations are probably reduced (c.f. Dembinski 1971) resulting in a higher predation on benthic animals. However the amount of food consumed by the smelts in winter was reduced, thus the total contribution of zoobenthos in the smelts' diet through the year is low. Lower consumption of food during winter is reported both for smelts (Belyanina 1969, Foltz and Norden 1977) and other fish species (Keast 1968). The low water temperatures reduce the metabolic rate, resulting in reduced activity of the fish and thus the need of food. In summer and autumn when the abundance of preferred zooplankton in Tyrifjorden is high (Tab. 2), the smelts change to a diet consisting mainly of pelagic crustaceans. Seasonal changes in food composition are also reported for other planktivorous fish species such as char *Salvelinus alpinus* (Nilsson 1955) and whitefish *Coregonus lavaretus* (Jacobsen 1974).

The smelts in Tyrifjorden clearly selected some of the zooplankton species, according to the selectivity index. However this index has limited validity for prey species with low occurrence in the habitat, when total number of individuals in all the stomachs (n_r) and in the habitat sample (n_p) are small (i.e. n_r, $n_p \leqslant 100$) (Strauss

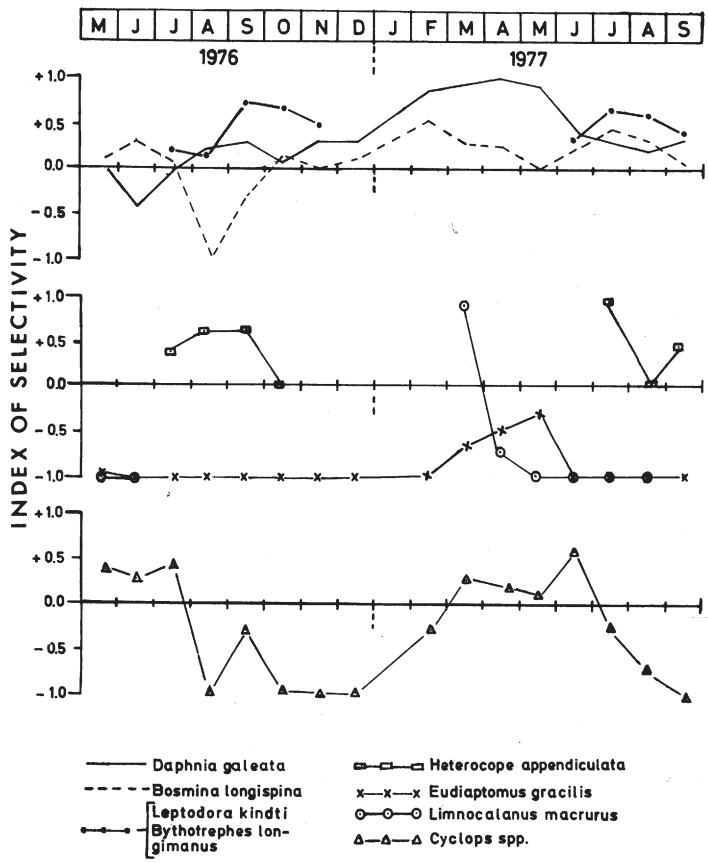

Fig. 3. Selectivity indices for zooplankton species by smelts in Tyrifjorden in 1976 and 1977.

1979). Confidence intervals are then quite wide, thus reducing the reliability of E. In this study n_r and n_p were large except in February, March, April, and May. The values of E calculated are therefore sufficiently reliable for proper evaluation in most of the samples, according to Strauss (op.cit.). Another factor which has influence on the selectivity index is different vertical distribution of the zooplankton species. Fish in the different water strata will prey upon different concentrations of zooplankton. The vertical distribution of the crustaceans in Tyrifjorden was not studied. However it was assumed that the smelts fed more or less randomly in the different water layers when rising towards the surface at night. The net hauls were therefore presumed to give an approximately right picture of the zooplankton available to the smelts.

Seasonal changes in predation and selection of zooplankton species by the smelts as observed in Tyrifjorden are also reported by Czeczuga (1959) and Belyanina (1969). The occurrence of different crustacean species in the plankton community varies during the year according to nutrients available, water temperature, competition and predation (Wetzel 1975). However abundance is not the main factor causing selection of the crustaceans by the fish. In Tyrifjorden *E. gracilis* were numerous through the year, but they were not selected by the smelts.

Diet analysis has indicated that planktivorous fish consume more large sized prey than if feeding were random (Brooks and Dodson 1965, Galbraith 1967, Berg 1970). This phenomenon is known as size-selective predation and implies an active choice by the fish in locating the prey by sight and sucking it into the mouth (Sbikin 1974, O'Brien 1979). Factors making the prey more visible such as body size, patterns of motion and pigmentation thus have a strong influence on selection by the fish (Brooks 1968, Zaret and Kerfoot 1975, Drenner et al. 1978, O'Brien

1979). In Tyrifjorden the smelts showed clear preference for cladocerans over copepods during most of the year. Copepods are often avoided by planktivorous fish when cladocerans are available (Lindström 1955, Berg and Grimaldi 1966, Hakkari 1978), which probably is a result of different patterns of motion. The copepods move only intermittently, and their agility (Allan 1976) may make capture difficult, while the slow, continually moving cladocerans are probably easier to locate and capture by the planktivores (O'Brien 1979).

The size of body and pigmented areas of the zooplankton specimens in the smelt stomachs were not studied, but these selection factors were obviously important also in Tyrifjorden. The copepod *H. appendiculata* and the cladocerans *D. galeata, L. kindti* and *B. longimanus,* which were the most selected crustaceans, were among the largest items in the zooplankton (Tab. 1) with large pigmented carapax and pigmented eye areas. This probably made them visible and therefore attractive to the smelts. Selection of these species has also been documented in other studies of smelts (Bergaust 1972, Hakkari 1978). *B. longispina* was however also selected by the smelts in spite of small body size (Tab. 1). In May and June 1976 the smelts even preferred *B. longispina* to *D. galeata* which was negatively selected. *B. longispina* may occur in swarms (Dumont 1967, Klemetsen 1970) which make them visible in spite of small body size. Eggs and juveniles in the brood pouch will also increase the probability of being detected by the smelts. These factors were however not studied.

The copepods except *H. appendiculata* were negatively selected by the smelts during most of the year in Tyrifjorden. Only in winter and spring when cladocerans, especially *D. galeata,* were less numerous, did the smelts prey upon *Cyclops spp* and *E. gracilis* to some extent. The smelts in Tyrifjorden seem therefore to select the zooplankton species which is most available with respect to body size, pigmentation and patterns of motion. Only when preferred prey items are rare, do the smelts change to other prey species. This change will only last till the more attractive species again are numerous in the zooplankton.

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REFERENCES

Allan, D.A. 1976. Life history patterns in Zooplankton. *Am. Nat. 110:* 165—180.

Anderson, T. 1968. Undersökingar av fiskebeståndet i Erken med hjälp av ekolod och trål. *Inform. Sötv. Lab. Drottningholm 12:* 1—24.

Belyanina, T.N. 1969. Synopsis of biological data on smelt *Osmerus eperlanus* (Linnaeus) 1738. *FAO Fish. Synops. (78).*

Berg, A. 1970. A comparative study of food and growth, and competition between two species of Coregonids introduced into Lake Maggiore, Italy. — In: Lindsey, C.C. and Woods, C.S. (eds.), *Biology of Coregonid Fishes.* Winnipeg, pp. 311—346.

Berg, A. and Grimaldi, E. 1966. Ecological relationship between planktophagic fish species in Lago Maggiore. *Verh. int. Ver. Limnol. 16:* 1065—1073.

Bergaust, O.P. 1972. Krøkla. (*Osmerus eperlanus eperlanus* L.) i Steinsfjorden. Ernæring, alder og vekst. *Unpubl. thesis,* Univ. of Oslo.

Bernardi, R. and Giussani, G. 1975. Population dynamics of three cladocerans of Lago Maggiore related to predation pressure by a planktophagous fish. *Ver. int. Ver. Limnol. 19:* 2906—2912.

Brooks, J.L. 1968. The effects of prey-size selection by lake planktivores. *Syst. Zool. 17:* 273—291.

Brooks, J.L. and Dodson, S.I. 1965. Predation, body size and composition of plankton. *Science 150:* 28—35.

Burbidge, R.G. 1969. Age, Growth, Length-Weight Relationship, Sex Ratio and Food Habits of American Smelt, *Osmerus mordax* (Mitchill), from Gull Lake, Michigan. *Trans. Amer. Fish. Soc. 98 (4):* 631—640.

Cooper, G.P. 1940. A biological survey of Rangely Lakes, with special references to the trout and salmon. *Fish. Surv. Rep. Me. 3:* 1—183.

Czeczuga, B. 1959. Stynka (*Osmerus eperlanus* L.) w Jez. Rajgrodzkim i jej biologia. *Pol. Arch. Hydrobiol. 5 (18):* 131—146.

Dembinski, W. 1971. Vertical distribution of *Coregonus albula* and other pelagic fish species in some Polish lakes. *J. Fish. Biol. 3:* 341—357.

Dumont, H.J. 1967. A five day study of patchiness in *Bosmina coregoni* Baird in a shallow, eutrophic lake. *Mem. Ist. Ital. Idrobiol 22:* 81—103.

Drenner, R.W., Strickler, J.R. and O'Brien, W.J. 1978. Capture probability: The role of zooplankton escape in selective feeding of planktivorous fish. *J. Fish. Res. Bd Canada 35:* 1370—1373.

Edmondson, W.T. 1971. Methods for Processing Samples and Developing Data. In: Edmondson, W.T. and Winberg, G.G. (eds.), *Secondary productivity in fresh waters. IBP-Handbook no 17,* Blackwell Sci. Publ., Oxford and Edinburgh, pp. 125—169.

Foltz, J.W. and Norden, C.R. 1977. Seasonal Changes in Food Consumption and Energy Content of smelt *(Osmerus mordax)* in Lake Michigan. *Trans. Amer. Fish. Soc. 106 (3):* 230—234.

Galbraith, M.G. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. *Trans. Amer. Fish. Soc. 96 (1):* 1—10.

Garnås, E. 1978. Ernæring, alder og vekst hos krøkle (*Osmerus eperlanus* L.) i Holstfjorden (del av Tyrifjorden). *Unpubl. thesis,* Univ. in Oslo.

Hakkari, L. 1978. On the productivity and ecology of zooplankton and its role as food for fish in some lakes i Central Finland. *Biol. Res. Rep. Univ. Jyväskylä 4:* 3—87.

Holtan, H. 1970. Tyrifjorden. En limnologisk undersøkelse 1967—1968. *Rapp. Norsk Inst. Vannforskning 0—15/64.*

Hynes, H.B.N. 1950. The food of fresh-water sticklebacks *(Gasterosteus aculeatus* and *Pygosteus pungitius),* with a review of the methods used in studies of food of fishes. *J. Anim. Ecol. 19 (1):* 36—58.

Hyslop, E.J. 1980. Stomach contents analysis — a review of methods and their application. *J. Fish. Biol. 17:* 411—429.

Ivlev, V.S. 1961. *Experimental ecology of the feeding of fishes.* Yale Univ. Press. New Haven Conn.

Jacobsen, O.J. 1974. Feeding habits of the population of whitefish (*Coregonus lavaretus* (L.)) in Haugatjern — a eutrophic Norwegian lake. *Norw. J. Zool. 22:* 295—318.

Jonasson, P.M. 1972. Ecology and Production of the Profundal Benthos in Relation to Phytoplankton in Lake Esrom. *Oikos Suppl. 14:* 1—148.

Keast, A. 1968. Feeding of some Great lakes fishes at low temperatures. *J. Fish. Res. Bd Can. 25:* 1199—1218.

Klemetsen, A. 1970. Plankton swarms in lake Gjøkvatn, east Finnmark. *Astarte 3:* 83—85.

Langeland, A. 1971. Biologiske undersøkelser i Holsfjorden (Tyrifjorden) 1971. *Rapport Norsk Inst. Vannforskning 0—143/70.*

Langeland, A. 1974. Long-term changes in plankton of Lake Tyrifjord, Norway. *Norw. J. Zool. 22:* 207—219.

Leskien, J. 1942. Beitrag zur Biologie des Stintes (*Osmerus eperlanus* L.). *Z. Fisch. 40 (1),*

Lindström, T. 1955. On the relation Fish size — Food size. *Rep. Inst. Freshw. Res. Drottningholm 36:* 132—147.

Man, H.S.H. and Hodgkiss, I.J. 1977. Studies on the ichthyofauna in Plover Cove Reservoir, Hong Kong: feeding and food relations. *J. Fish Biol. 11:* 1—13.

Milbrink, G. 1973. Fiskens näringsval i Ekoln — en sammenfattning av tre delundersökningar. *Inform. Inst. Freshw. Res. Drottningholm 6:* 1—12.

Nilsson, N.A. 1955. Studies on the feeding habits of trout and char in North Swedish lakes. *Rep. Inst. Freshw. Res. Drottningholm 36:* 163—225.

Nyhagen, O.J. 1959. En limnologisk undersøkelse av Holsfjorden. *Unpubl. thesis,* Univ. of Oslo.

Nordquist, O. 1910. Zur biologie des Stintes *(Osmerus eperlanus* L.). *Acta Soc. pro Fauna et Flora Fennica 33,* 1—18.

Northcote, T.G. and Rundberg, H. 1970. Spatial distribution of pelagic fishes in Lambarfjärden (Mälaren Sweden) with particular reference to interaction between *Coregonus albula* and *Osmerus eperlanus. Rep. Inst. Freshw. Res. Drottningholm 50:* 133—167.

O'Brien, W.J. 1979. The Predator — Prey Interaction of Planktivorous Fish and Zooplankton. *Amer. Scientist 67:* 572—581.

Rembiszewski, J.N. 1970. Populations variation in smelt — *Osmerus eperlanus* (Linnaeus 1758) (Pisces) in Poland. *Ann. Zool. 28:* 65—95.

Sandlund, O.T., Klyve, L., Hagen, H. and Næsje, T.F. 1980. Krøkla i Mjøsa. Alderssammensetning, vekst og ernæring. *DVF-Mjøsundersøkelsene Rapport nr. 2:* 70 pp.

Sbikin, Yu. N. 1974. Age-related changes in the role on vision in the feeding of various fishes. *J. Ichthyol. 14 (1):* 133—139.

Strauss, R.E. 1979. Reliability estimates for Ivlev's Electivity Index, the Forage Ratio, and a proposed linear index of food selection. *Trans. Am. Fisch. Soc. 108:* 344—352.

Strøm, K.M. 1932. Tyrifjord. A limnological study. *Skr. norske Vidensk. Akad. Mat. Naturv. 3:* 1—84.

Svärdson, G. 1976. Interspecific Population Dominance in Fish Communities of Scandinavian Lakes. *Rep. Inst. Freshw. Res. Drottningholm 55:* 144—171.

Wetzel, R.G. 1975. *Limnology.* W.B. Saunders Company, Toronto, Canada: 1—743.

Willer, A. 1926. Untersuchungen über den Stint, *Osmerus eperlanus,* in Ostpreuszen. *Z. Fisch. 24 (4):* 521—558.

Zaret, T.M. and Kerfoot, W.C. 1975. Fish predation on *Bosmina longirostris:* Body-size selection versus visibility selection. *Ecology 56:* 232—237.