

Habitat Switch and Niche Overlap in Coregonid Fishes: Effects of Zooplankton Abundance

T. F. Næsje, B. Jonsson, and O. T. Sandlund

Norwegian Institute for Nature Research, Tungasletta 2, N-7004 Trondheim, Norway

and G. Kjellberg

Norwegian Institute for Water Research, Regional Office Østlandet, Rute 866, N-2312 Ottestad, Norway

Næsje, T. F., B. Jonsson, O. T. Sandlund, and G. Kjellberg. 1991. Habitat switch and niche overlap in coregonid fishes: effects of zooplankton abundance. *Can. J. Fish. Aquat. Sci.* 48: 2307–2315.

Vendace (*Coregonus albula*) in Lake Mjøsa lived in the pelagic zone and gillnet catches were correlated with water temperature ($r^2 = 0.457$, $p < 0.005$). Whitefish (*Coregonus lavaretus*) exploited both epibenthic and pelagic areas. Whitefish with body lengths between 25 and 35 cm moved from the epibenthic to pelagic zone during summer; other length groups remained in epibenthic habitats. The pelagic fish returned to epibenthic areas in the autumn. Cladocerans were important food items for both fish species in the pelagic zone. The large copepod *Limnocalanus macrurus* was eaten only by vendace whereas surface insects were more important prey for whitefish. This suggests that vendace is the more specialized zooplanktivore. The pelagic gillnet catch of whitefish and the pelagic habitat overlap between whitefish and vendace increased with increasing zooplankton densities at depths between 0 and 50 m ($r^2 = 0.609$ and 0.494 , respectively, $p < 0.01$). During spring and autumn we observed a time lag between the change in zooplankton abundance and habitat switches of whitefish. The fish moved to the more profitable habitat several days after food availability had changed, indicating an element of learning in choice of habitat.

Le corégone blanc (*Coregonus albula*) du lac Mjøsa vivait dans la zone pélagique et les prises au filet maillant ont été corrélées avec la température de l'eau ($r^2 = 0,457$, $p < 0,005$). Le lavaret du Bourget (*Coregonus lavaretus*) a exploité les zones épibenthiques et pélagique. Les lavarets de 25 à 35 cm de long se déplaçaient de la zone épibenthique à la zone pélagique en été; les groupes de longueur différents demeuraient dans des habitats épibenthiques. Ce poisson pélagique retournait dans des zones épibenthiques à l'automne. Les deux espèces de poisson se nourrissaient surtout de cladocères dans la zone pélagique. Le grand copépode *Limnocalanus macrurus* n'était mangé que par le corégone blanc, tandis que les insectes de surface étaient des proies plus importantes pour le lavaret. Cela indique que le corégone blanc est le zooplanctivore plus spécialisé. Les prises de lavaret pélagique du corégone blanc et du lavaret ont augmenté avec la concentration croissante de zooplancton à des profondeurs de 0 à 50 m ($r^2 = 0,609$ et $0,494$ respectivement, $p < 0,01$). Pendant l'été et à l'automne, nous avons observé un décalage de temps entre les variations d'abondance du zooplancton et les changements d'habitat du lavaret. Le poisson s'est déplacé dans l'habitat le plus propice plusieurs jours après que la nourriture vint à manquer, dénotant un élément d'apprentissage dans le choix d'habitat.

Received November 19, 1990
Accepted June 26, 1991
(JA811)

Reçu le 19 novembre 1990
Accepté le 26 juin 1991

Seasonal habitat switches of animals are supposed to result from changes in the environmental conditions, and habitat choices are considered to be trade-offs between profitabilities and risks in the environment (Stephens and Krebs 1986). Solitary animals will move from one food patch to another in order to maximize their energy gains (Charnov 1976), and animals may evaluate profits and costs of different habitats (Dill 1987; Werner and Hall 1988). Behaviour of fish may be modified by the process of learning about the quality of food patches (Milinski 1984; Werner and Hall 1988), by the risk of predation (Werner et al. 1983; Mittelbach 1984; Holbrook and Schmitt 1988), and by the presence of competitors (Pitcher et al. 1982).

In northern temperate lakes, prey abundance fluctuates seasonally and is an important factor influencing temporal habitat switches of fish. In many lakes, whitefish (*Coregonus lavaretus*) may exhibit seasonal habitat switches between benthic and pelagic habitats (Svärdson 1976). The closely related ven-

dace (*Coregonus albula*) is usually pelagic when cooccurring with whitefish (Svärdson 1976; Nilsson 1979). In such situations the two fish species segregate in food selection (Hamrin and Persson 1986). Vendace is the more specialized zooplankton feeder whereas whitefish is a more generalized feeder, exploiting both epibenthic and pelagic food resources (Svärdson 1976; Hamrin and Persson 1986). Little is known, however, about the seasonal and spatial habitat use of these fishes in relation to pelagic food abundance.

Thus we studied habitat use of vendace and whitefish in Norwegian Lake Mjøsa where we tested (1) if habitat shifts of whitefish between epibenthic and pelagic habitats were correlated with the abundance of crustacean zooplankton, (2) if habitat overlaps between whitefish and vendace were correlated with the abundance of crustacean zooplankton, and (3) if diet overlaps between whitefish and vendace were correlated with the abundance of crustacean zooplankton.

TABLE 1. Mean annual CPUE of the most important fish species in Lake Mjøsa, 1978–80 (after Sandlund et al. 1985).

Species	Pelagic nets	Benthic nets
Brown trout (<i>Salmo trutta</i>)	0.1	<<0.1
Vendace (<i>Coregonus albula</i>)	0.9	0.1
Whitefish (<i>Coregonus lavaretus</i>)	0.4	1.4
Smelt (<i>Osmerus eperlanus</i>)	2.4	5.1
Roach (<i>Rutilus rutilus</i>)	<<0.1	3.4
Perch (<i>Perca fluviatilis</i>)	<<0.1	2.1
Ruffe (<i>Acerina cernua</i>)	<<0.1	4.3
Northern pike (<i>Esox lucius</i>)	<<0.1	<<0.1
Burbot (<i>Lota lota</i>)	0.0	0.9

Methods

Study Site

Mjøsa (61°30'N, 10°25'E) is a 449-m-deep oligomesotrophic, dimictic fjord lake and has a surface area of 365 km². The circulation periods last from late April until the end of June and from October until ice cover, usually in January–February (Holtan 1979). The thermocline is established at 12–20 m depth. In 1979, hypolimnetic temperatures varied between 3.5 and 8°C. Epilimnetic temperatures reached 10°C by the middle of June and a maximum of 14°C in July. Total pelagic primary production in 1979 was approximately 20 g C·m⁻²·yr⁻¹ (Kjellberg and Sandlund 1983).

A total of 20 crustacean zooplankton species occur in the pelagic zone in Mjøsa; 8 are copepods and 12 are cladocerans (Holtan et al. 1980). The most common are the copepods *Limnocalanus macrurus* Sars, *Eudiaptomus gracilis* Sars and *Cyclops lacustris* Sars and the cladocerans *Daphnia galeata* Sars, *D. cristata* Sars, and *Bosmina longispina* Leydig (Sandlund et al. 1991a).

Zoobenthos is dominated by chironomid larvae, oligochaetes, bivalves, and the amphipods *Pallasea quadrispinosa* Sars and *Gammaracanthus loricatus* Sabine (Holtan et al. 1980). *Mysis relicta* Lovén occurs in both epibenthic and pelagic habitats (Kjellberg and Sandlund 1983). Among zoobenthos eaten by epibenthic whitefish, chironomid larvae and pupae and *P. quadrispinosa* are the most important.

Mjøsa supports 20 fish species, with vendace, whitefish, and smelt (*Osmerus eperlanus*) being numerically dominant in the pelagic zone (Sandlund et al. 1985) (Table 1). In shallow water, roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), and ruffe (*Acerina cernua*) are the most numerous. The main predators are brown trout (*Salmo trutta*), burbot (*Lota lota*), and northern pike (*Esox lucius*).

Vendace and whitefish grow at about the same rate during the first 2 yr of life, reaching 11–12 cm at age 1 and 18–20 cm at age 2. The growth rate of vendace levels off earlier than for whitefish; asymptotic lengths and Brody's coefficient of the von Bertalanffy growth equations were respectively 22.7 cm and 1.03 for vendace and 31.0 cm and 0.52 for whitefish. The growth rate of males and females did not differ significantly ($p > 0.05$) (Næsje et al. 1986; Sandlund et al. 1991a).

Sampling

Zooplankton (February–December 1979), benthic insects and molluscs (May–November 1979), and fish (October 1978 – February 1980) were sampled at two localities in Mjøsa: Brøttum and Furnes. In both areas, maximum depth is around 90 m.

Zooplankton were sampled with a 25-L Schindler trap at the following depths: 0.5, 2, 5, 8, 10, 12, 16, 20, 30, and 50 m. One sample was taken at each depth (Langeland and Rognerud 1974) and subsequently identified and counted in an inverted microscope.

Benthic invertebrates were sampled with an Ekman grab (0.025 m², 0.5-mm bar mesh in screen) at the following depths: 0.5, 2, 4, 6, 8, 12, 20, and 50 m. The 0.5- and 2-m samples were omitted due to a stony substratum causing the Ekman grab to malfunction. Three replicate samples were taken at each depth in both sampling areas. Zoobenthos abundance was calculated as mean number and wet weight (grams) of animals per square metre, adjusted for the relative area of the sampled depth zones.

Fish were sampled by using epibenthic and pelagic gill nets. The gill nets consisted of 12 panels (panel size: epibenthic 25 × 2 m; pelagic 25 × 6 m) with varying mesh sizes (8- to 52-mm bar mesh, mesh increments 2–7 mm). Fish were sampled one to five 24-h periods at two pelagic and four epibenthic stations each month (except for December when only pelagic nets were used and January and March when sampling was omitted). The pelagic nets were placed at the following depths: 0–10, 10–30, 30–50, and 50–80 m. The epibenthic nets were set from the shoreline down to the deepest part of the sampling area (90 m). The exact depth of each net was registered with an echo sounder (Simrad EL). Catch per unit effort (CPUE) was calculated as number of fish per 100 m² of net area for 24 h of fishing.

Laboratory and Data Analyses

Fish were measured to the nearest 0.1 cm (natural tip length, Ricker 1979) and aged by burning and breaking the otoliths (Christensen 1964).

Stomach contents were analyzed and prey categories identified and counted under a stereoscopic microscope. Wet weight of stomach contents was estimated from undigested food items. The degree of diet overlap was calculated according to Schoener's (1968) similarity index $D = 1 - 1/2 \sum_{i=1}^n |p_i - q_i|$ where

p_i is the weight proportion of food item i in population 1, q_i is the weight proportion of food item i in population 2, and n is the number of food categories. Index D varies between 0 and 1, representing no and complete food overlap, respectively. Degree of habitat overlap in the pelagic zone was calculated using Schoener's (1968) index, letting p_i and q_i represent the percentage of vendace and whitefish at the i th depth zone relative to the respective depth distributions of the species.

Zooplankton selection was estimated according to Ivlev's (1961) electivity index $E = (a - b)/(a + b)$ where a is the frequency by number of the prey organism in the stomach and b is the frequency by number of the prey organism in the environment.

Results

Zooplankton

The zooplankton community was dominated by *L. macrurus* (spring) and *E. gracilis*, *B. longispina*, *D. galeata*, and *D. cristata* (summer and early autumn) (Fig. 1). Densities of zooplankton were generally higher at Furnes than at Brøttum. At Furnes, maximum biomass of crustacean zooplankton occurred in August (6400 mg·m⁻²) and at Brøttum in July (2400 mg·m⁻²). At Furnes, maximum densities of adult *D. galeata* were recorded in August (7780 ind·m⁻³) and

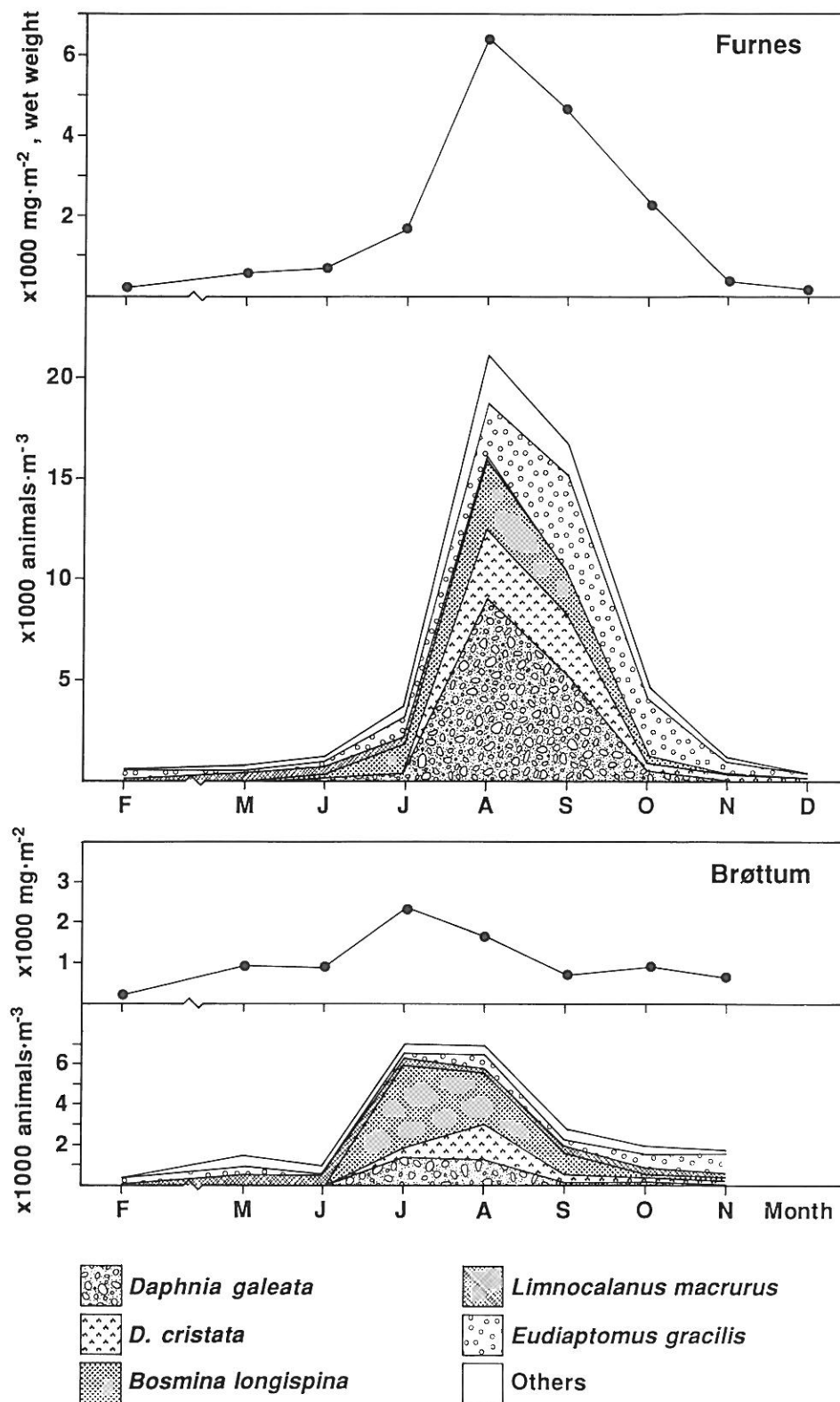


FIG. 1. Number of crustacean zooplankton in the 0–50 m depth zone in the sampling areas Furnes and Brøttum in Mjøsa, February–December 1979. Copepod nauplii and cladoceran embryos were omitted.

September (5100 ind·m⁻³). At Brøttum, densities of *D. galeata* were lower, with largest numbers of adults in July (1040 ind·m⁻³) and August (940 ind·m⁻³). At Furnes, *B. longispina* occurred in maximum densities in July

(1320 ind·m⁻³), August (2880 ind·m⁻³), and September (1360 ind·m⁻³). Densities of *B. longispina* at Brøttum were higher, with maximum numbers in July (3220 ind·m⁻³), August (2240 ind·m⁻³), and September (1010 ind·m⁻³).

TABLE 2. Abundance (N , no. $\cdot m^{-2}$) and wet weight (w , $g \cdot m^{-2}$) (mean and standard deviation) of benthic insects and molluscs in the sampling areas Furnes and Brøttum in Mjøsa, 1979.

Month	Furnes				Brøttum			
	N	SD	w	SD	N	SD	w	SD
May	407.9	8.7	0.36	0.05	471.9	27.2	0.87	0.55
July	530.1	143.3	1.78	0.82	353.9	141.6	0.32	0.15
August	250.5	34.9	0.46	0.16	243.8	28.0	0.25	0.03
October	254.9	124.4	0.43	0.22	304.7	117.8	0.59	0.30
November	457.5	121.4	0.78	0.19	239.6	78.0	0.34	0.12

Zoobenthos

The zoobenthos in Mjøsa, as shown by Ekman grab samples, was dominated by chironomid larvae on most sampling dates (Holtan et al. 1980). Oligochaetes, the molluscs *Pisidium*, and the amphipode *P. quadrispinosa* were also common. Being a very mobile animal, *P. quadrispinosa* is able to avoid most zoobenthos samplers, and it was not sampled representatively with an Ekman grab.

The zoobenthos abundance in terms of wet weight and number of animals was highest in shallow waters (<10 m depth). The abundance and biomass of insects and molluscs, which were the zoobenthos groups eaten by whitefish, reached a maximum in July at Furnes and in May at Brøttum (Table 2).

Vendace and Whitefish

Habitat

A total of 1172 vendace and 1161 whitefish were caught. Very few whitefish and vendace were caught deeper than 50 m in the pelagic zone. Gill net catches of vendace were low in winter, spring, and early summer (November – July) (Fig. 2A). In epibenthic habitat CPUE of vendace remained low through the rest of the year, except for a slight increase in October at Brøttum, situated near the spawning grounds. CPUEs in the pelagic habitat, however, were high in late summer and autumn (August – October) (Fig. 2A). In June – July, pelagic vendace were mainly caught at depths between 0 and 10 m, but from August through November they were also abundant at depths between 10 and 30 m.

Whitefish were caught in both benthic and pelagic habitats (Fig. 2B). In the epibenthic habitat, mean CPUE of whitefish varied between 0.80 and 1.54. The pelagic catches of whitefish were very low during winter, spring, and early summer but increased during late summer and autumn. In both sampling areas, Brøttum and Furnes, a part of the whitefish population started to move into the pelagic habitat in July whereas maximum pelagic catches were taken in September (Fig. 2B). In November, most of the whitefish had returned to the epibenthic habitat. Pelagic densities of whitefish were highest at depths between 0 and 30 m.

Diet

In the pelagic zone, the diet of vendace and whitefish differed between the sampling areas (Fig. 3). At Furnes, vendace fed largely on the zooplankton species *B. longispina*, *D. galeata*, and *L. macrurus*. At Brøttum, vendace fed on the same food items, but the relative proportions were different. *Daphnia galeata* was less important whereas *L. macrurus* was more important as a food source (Mann–Whitney tests, $p < 0.05$). In addition, vendace at Brøttum also fed on *Leptodora kindti* (Focke) and fish (age 0 smelt).

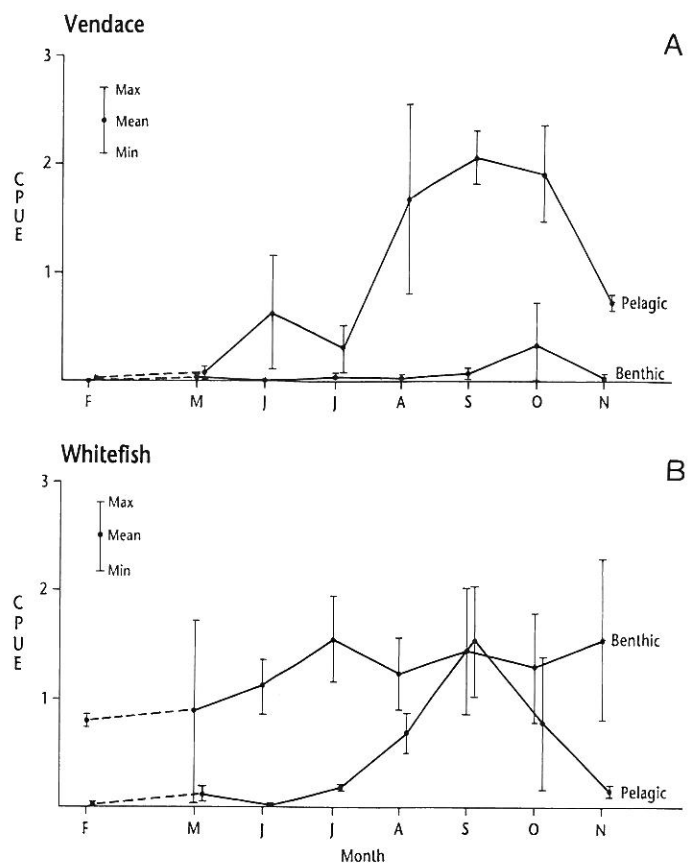


FIG. 2. CPUE of (A) vendace and (B) whitefish in pelagic and benthic gill nets, February–November 1979.

Whitefish fed largely on zooplankton in the pelagic zone (Fig. 3). At Furnes the most important zooplankters eaten were *L. kindti* and *D. galeata*. In addition, they fed on surface arthropods and fish (age 0 smelt). At Brøttum, whitefish fed on the same food items, but in addition, cyclopoid copepods were a more important food source. Whitefish caught in the pelagic zone appeared to stay in that zone for some time, as the frequency of bottom animals in their stomachs was very low. A small fraction of the amphipod *P. quadrispinosa*, however, indicated some exchange of fish between epibenthic and pelagic areas.

Based on estimates of Ivlev's (1961) electivity indices, vendace and whitefish appeared to differ in their selection of *L. macrurus* (Fig. 4). This species was positively selected by vendace during spring and late summer and autumn but was never selected by whitefish. Both vendace and whitefish selected *B. longispina* and *D. galeata* during summer and autumn, respectively. The large cladocerans *L. kindti* and *Bythotrephes longimanus* Leydig were also positively selected for shorter periods during summer. All other zooplankters were negatively selected.

Correlations in habitat and diet

The pelagic catches (CPUE) of vendace were more highly correlated with epilimnic water temperature (0–16 m) than with abundance of pelagic food, expressed as total number of crustacean zooplankton in 0–50 m depth (temperature: $r^2 = 0.457$, $p = 0.004$; zooplankton no.: $r^2 = 0.337$, $p = 0.018$) (Fig. 5A). On the other hand, the pelagic catches (CPUE) of whitefish showed higher correlation with number of crustacean

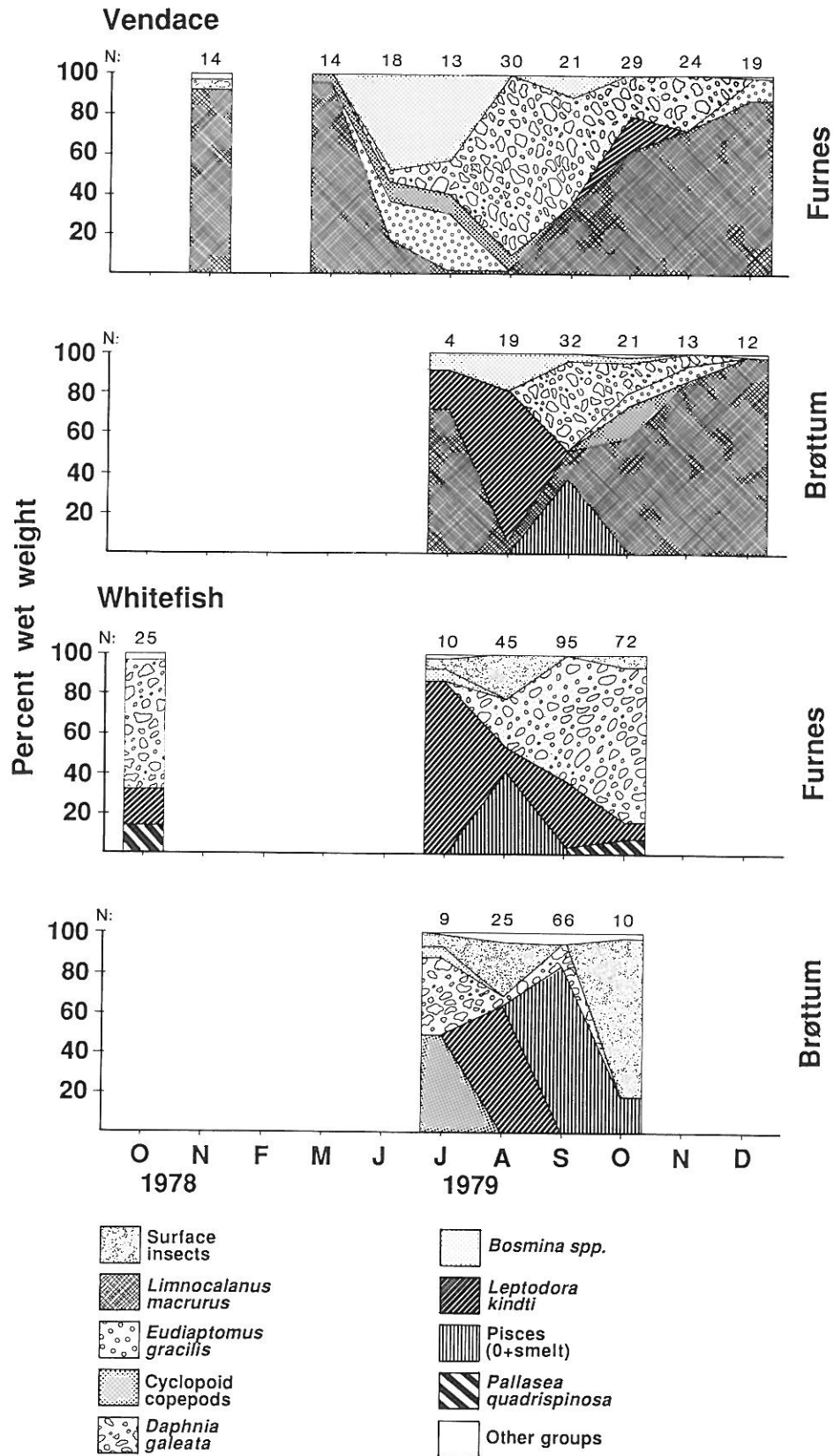


FIG. 3. Composition of stomach contents of pelagic vendace and whitefish in the sampling areas Furnes and Brøttum in Mjøsa, 1979.

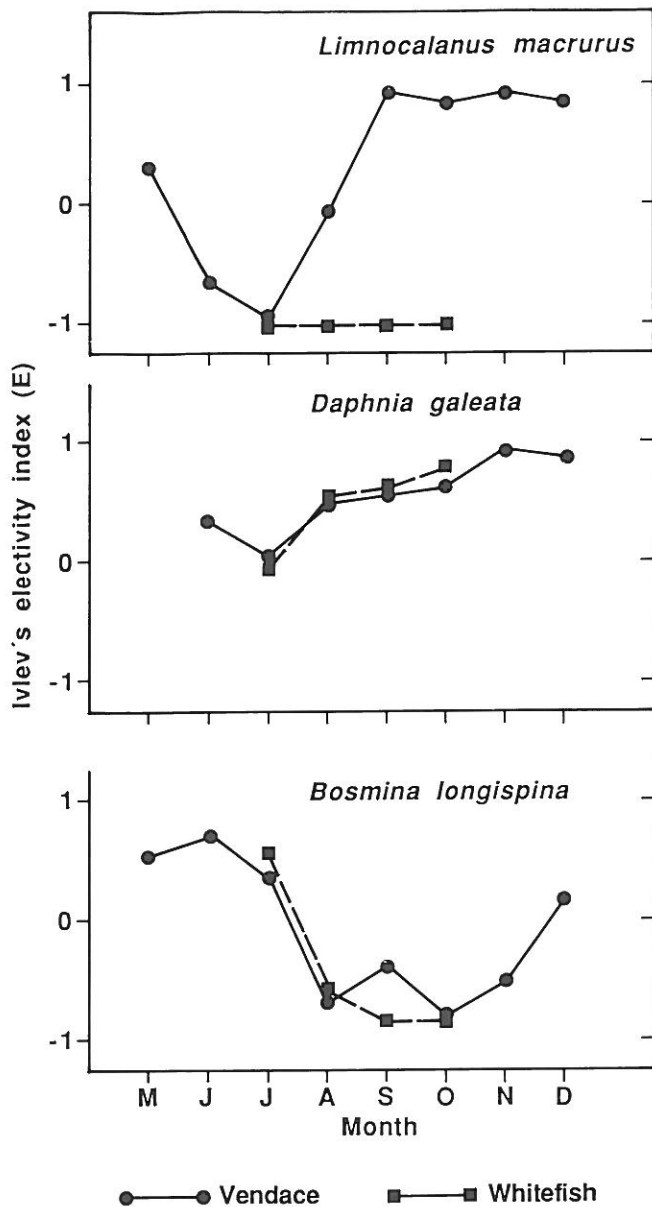


FIG. 4. Ivlev's electivity index (E) for the selection of three crustacean zooplankton species by pelagic whitefish (squares) and vendace (circles) at Furnes, May–December 1979.

zooplankton than with the epilimnic water temperature (temperature: $r^2 = 0.503$, $p = 0.002$; zooplankton no.: $r^2 = 0.609$, $p = 0.0004$) (Fig. 5B). Water temperature and total number of crustacean zooplankton, however, were intercorrelated ($r^2 = 0.737$, $p = 0.0001$). The two regressions ($CPUE_{whitefish}$ on zooplankton abundance and $CPUE_{vendace}$ on epilimnic water temperature) were not improved by adding water temperature and zooplankton, respectively, as a second independent variable in multiple regression models.

Figure 5B gives the regression of pelagic catch of whitefish over total number of crustacean zooplankton. Points above the regression line represent months where CPUEs were higher than expected from the number of zooplankton, and points below represent months when the catch was lower. It can be noted that the points are below the line in June and July when the abundance of zooplankton was increasing and above the line in September and October after the abundance had passed its max-

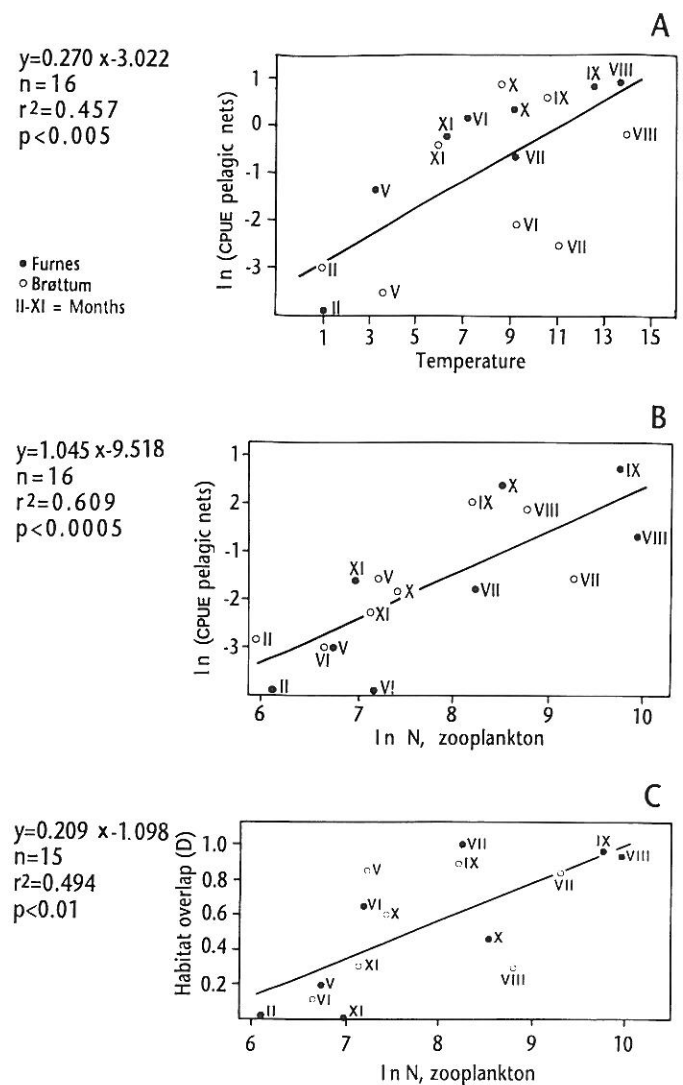


FIG. 5. (A) Linear regression of $\ln(\log_e)$ CPUE of vendace in pelagic gill nets on water temperature, 0–16 m depth. (B) Linear regression of $\ln(\log_e)$ CPUE of whitefish in pelagic gill nets on $\ln(\log_e)$ of number of crustacean zooplankton cubic metre, 0–50 m depth. (C) Linear regression of pelagic habitat overlap between vendace and whitefish (Schoener's (1968) index D) on $\ln(\log_e)$ of number of crustacean zooplankton cubic metre, 0–50 m depth.

imum and was decreasing. The \ln -transformed curves fitted for cladocerans and copepods separately gave $r^2 = 0.568$ and 0.458 ($P < 0.01$), respectively. The pelagic catch also increased with the biomass of crustacean zooplankton (0–50 m), but the fit was not as good as for total numbers ($r^2 = 0.477$, $p < 0.01$).

Neither the pelagic nor the benthic catches of whitefish were significantly ($p > 0.05$) correlated with the abundance or wet weight of insects and molluscs in the benthic habitat (Table 2), the main zoobenthos eaten by the fish (except *P. quadrispinosa* which was not sampled by the Ekman grab). Similar results ($p > 0.05$) were found for the regressions of whitefish catches on total zoobenthos abundance and wet weight.

In most sampling periods there was a high vertical habitat overlap between whitefish and crustacean zooplankton and vendace and crustacean zooplankton in the pelagic habitat (Table 3). In periods with more than 15 fish caught, Schoener's

TABLE 3. Vertical habitat overlap between whitefish and zooplankton and vendace and zooplankton (Schoener's (1968) index *D*) in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, May – November 1979 (number of fish in parentheses).

	May	June	July	Aug.	Sept.	Oct.	Nov.
Furnes							
Whitefish	0.521 (3)	0.651 (2)	0.710 (11)	0.715 (58)	0.683 (119)	0.788 (83)	0.253 (12)
Vendace	0.184 (17)	0.893 (76)	0.704 (34)	0.667 (289)	0.679 (132)	0.508 (89)	0.551 (48)
Brøttum							
Whitefish	0.216 (14)	0.250 (3)	0.954 (15)	0.418 (59)	0.788 (72)	0.769 (11)	0.577 (7)
Vendace	0.073 (2)	0.670 (8)	0.834 (5)	0.799 (57)	0.908 (127)	0.490 (213)	0.298 (45)

TABLE 4. Vertical habitat overlap (Schoener's (1968) index *D*) between vendace and whitefish in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, February–November 1979.

	Feb.	May	June	July	Aug.	Sept.	Oct.	Nov.
Furnes	0.000	0.202	0.658	0.994	0.952	0.958	0.295	0.133
Brøttum	—	0.857	0.117	0.833	0.297	0.880	0.603	0.298

(1968) index *D* was lower than 0.5 for whitefish in August at Brøttum and for vendace in May at Furnes and during the spawning run in October and November at Brøttum. Including all periods with more than 10 fish caught of each fish species, there was no significant difference in the habitat overlap of the two fish species, whitefish and vendace, and crustacean zooplankton (Mann–Whitney *U*-test, $p > 0.05$).

The vertical habitat overlap (Schoener's (1968) index) between whitefish and vendace in the pelagic zone at Furnes was high ($D > 0.6$) during June – September and low during the rest of the sampling period ($D < 0.3$) (Table 4). The index at Brøttum was high during July–October and in May and low in June, August, and November. The habitat overlap increased with increasing number of crustacean zooplankton per cubic metre at 0–50 m depth ($r^2 = 0.494$, $p < 0.01$; Fig. 5C) and with the biomass of zooplankton at 0–50 m depth, although this fit was somewhat lower ($r^2 = 0.462$, $p < 0.01$).

Diet overlap (Schoener's (1968) index) between vendace and whitefish at Furnes was highest in September and lowest in July (Table 5). At Brøttum the diet overlap was highest in August and lowest in October. There was no significant correlation ($p > 0.05$) between diet overlap and habitat overlap or diet overlap and the abundance of different categories of zooplankton.

Discussion

The increase in pelagic gillnet catches of whitefish from May until September indicated a movement of whitefish from epibenthic to pelagic areas. The same movement of whitefish was indicated by density estimates based on echo soundings (T. Lindem, Institute of Physics, University of Oslo, P.O. Box 1048, Blindern, N-0316 Oslo 3, Norway, pers. comm.). The number of pelagic fish of whitefish size (25–35 cm in length) increased from 24 fish·ha⁻¹ in May to a maximum of 182 fish·ha⁻¹ in September and decreased to a minimum of 21 fish·ha⁻¹ in November. During summer, pelagic whitefish probably remained in offshore areas for considerable periods of time

TABLE 5. Diet overlap (Schoener's (1968) index *D*) between vendace and whitefish in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, July–October 1979.

	July	Aug.	Sept.	Oct.
Furnes	0.076	0.236	0.551	0.289
Brøttum	0.056	0.648	0.516	0.008

because few of the pelagic whitefish caught had remains of zoobenthos in their stomachs. All through the year, whitefish of all length groups stayed in the epibenthic habitat feeding on benthic invertebrates (Sandlund et al. 1991b).

Both gillnet catches and echo soundings indicated that vendace exploit pelagic waters all year round (T. Lindem, pers. comm.). The pelagic CPUEs were more highly correlated with epilimnic temperatures than with the abundance of zooplankton, opposite to what was observed for pelagic whitefish. Therefore, variations in pelagic CPUE of vendace with time may be mainly due to differences in temperature-dependent activity. Vendace probably have a higher preferred temperature than whitefish (Valtonen 1970), although in the literature, evidence supporting this suggestion is meagre.

The CPUE of pelagic whitefish was more highly correlated with both water temperature and biomass of zooplankton than the corresponding relationships for vendace. This was probably because the catch of pelagic whitefish depended both on fish movement between epibenthic and pelagic areas and activity related to water temperature. Vendace, on the other hand, was chiefly exhibiting temperature-dependent activity in the pelagic zone (except for adult fish during autumn on the spawning grounds).

When fish assess the profitability of alternative feeding habitats, a process of learning is probably involved (Werner et al. 1983). Werner and Hall (1988), citing Ehlinger (1986), maintained that when bluegill (*Lepomis macrochirus*) were fed prey from one habitat and switched to prey from another habitat, they suffered nearly a 50% decrease in capture rates on the original prey type, as the new prey type was added to the diet. According to Werner and Hall (1988), learning and search image type phenomena prevented maximum efficiency on both prey types simultaneously.

If learning is involved in the habitat switch of whitefish in Mjøsa, a delay in fish movement relative to the increase in zooplankton abundance was anticipated. This is supported by our results showing that in the period with increasing abundance of zooplankton, CPUE of pelagic whitefish was lower than expected. On the other hand, the CPUE was above the expected value in the period with decreasing abundance of zooplankton. The fish may need some time to learn that food availability has changed, and accommodate to the new situation. In bluegill, Werner et al. (1981) indicated that the time lag between increase in food abundance and habitat change is about 1 wk. A similar time lag was found for Arctic char (*Salvelinus alpinus*) in seven natural lakes in Norway (Langeland et al. 1991). Such a learning mechanism has been described in a simple model called the Relative Payoff Sum (RPS) (Harley 1981; Regelman 1984). Switching to feeding on zooplankton in the pelagic zone paid off for the first whitefish trying this option when zooplankton densities were high. When zooplankton densities decreased in autumn, whitefish performed an opposite migration back to the, by then, more profitable epibenthic zone. There is, however, still little evidence indicating how learning regulates feeding behaviour of organisms, e.g. to what degree

animals have and use detailed quantitative information about their resources, and to what degree they depend on simpler rules of thumb when they select habitat and prey (Milinski 1984, 1986; Stephens and Krebs 1986).

An alternative to abundance of zooplankton as the explanation to the delay in habitat switch may be that it is influenced by abundance of zoobenthos. We did not, however, find any significant correlation between CPUE of benthic whitefish and the abundance of benthic insects and molluscs which are important food items for the epibenthic whitefish (Sandlund et al. 1991b). A more detailed analysis of all benthos groups might reveal some significant correlations between benthic food supply (e.g. *P. quadrispinosa*) and CPUE of benthic whitefish. We did not, however, have sufficient quantitative zoobenthos data to exploit this possibility.

Ehlinger (1990) found that bluegill selected foraging habitats as a function of the difference in foraging return rates between habitats. The fish spent the longest time in a habitat where the energetic return rate was highest. Our results indicate that within a species the return rate may differ between different size groups. In Mjøsa, medium-sized whitefish (25–35 cm) move into the pelagic zone during summer and autumn whereas smaller and larger fish remain in epibenthic areas. This may be explained by foraging theory, as the smaller fish stay in the more sheltered, epibenthic habitat where predation probably is lower than in the unstructured pelagic zone (Crowder and Cooper 1982; Stephens and Krebs 1986). The large, mobile, epibenthic amphipod *P. quadrispinosa* (8–18 mm in length) is a suitable food item for large whitefish (Næsje 1984; Sandlund et al. 1991b). Feeding on this prey may be more profitable than zooplankton for large fish. There seems to be very little predation on large whitefish in the lake.

In Mjøsa, habitat but not diet overlap between pelagic whitefish and vendace increased with increasing abundance of zooplankton. This might be an indication of exploitative competition, similar to what has been found in sunfishes (Werner and Hall 1979; Werner et al. 1977). Exploitative competition between two species occurs when one species reduces available food supply to a level making the habitat unprofitable for the other species (Werner and Hall 1976, 1977). In Mjøsa the efficient zooplanktivore vendace (Svårdson 1976) may have rendered the pelagic zone an unprofitable feeding habitat for whitefish, except in periods of maximum zooplankton density. Segregation by habitat rather than by diet seems to be the common means of resource partitioning among animal species (Schoener 1974; Schmitt and Coyer 1983). Interference competition, on the other hand, is not easily envisaged in the pelagic zone, as it often involves some aggressive behaviour, e.g. territoriality (Schutz and Northcote 1972; Hindar et al. 1988).

The habitat switches of whitefish and habitat overlap between vendace and whitefish were more highly correlated with number than biomass of zooplankton. These results may indicate that the fish respond to numbers rather than biomass of zooplankton. To be conclusive, however, supporting experimental data are needed.

Whitefish and vendace feed to some extent on the same zooplankton species, and select the same sizes within the species (Sandlund et al. 1987). However, their diet overlap (Schoener's (1968) index *D*) was never above 0.65. This was due to the fact that pelagic whitefish also utilize two other pelagic food sources which are abundant during summer: surface insects and age 0 smelts. Vendace, on the other hand, ate the copepods *L. macrurus* and *E. gracilis* which are not utilized by whitefish.

Copepods are generally considered difficult to catch for nonspecialist zooplanktivores (Szlauer 1965; Wright and O'Brien 1984). The difference in trophic morphology (cf. Nikolsky 1963) of the two species reflects the specialist versus the generalist: vendace has a superterminal mouth and dense gillrakers whereas whitefish has a subterminal mouth and sparse gillrakers (mean number of gillrakers 47 and 30, respectively; Sandlund et al. 1987). Whitefish, being the more generalized feeder, performed a habitat shift in relation to the zooplankton abundance whereas vendace, being the more specialized zooplankton feeder, occupied pelagic waters throughout the year.

Acknowledgements

We thank Leif Gjestad, Helge Hagen, and Gerd Justås for assistance in the field and laboratory and the staff at the Norwegian Institute for Nature Research's graphic unit for drawing the figures. The Directorate of Nature Management, Norwegian Institute for Nature Research, and the Norwegian Institute for Water Research provided financial support.

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