

Ontogenetic changes in habitat use by whitefish, *Coregonus lavaretus*

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Received 13.7.1990 Accepted 18.12.1990

Key words: Habitat use, Diet, Growth, Zooplankton, Zoobenthos, *Pallasea quadrispinosa*

Synopsis

The whitefish, *Coregonus lavaretus*, in the lake Mjøsa exhibited two niche changes during their life cycle. Juveniles (< 25 cm body length) were confined to the shallow (0–30 m) epibenthic zone. Medium sized whitefish (25–35 cm body length) expanded their habitat use to include the deep (30–90 m) epibenthic zone as well as the pelagic zone. From a body length of 35 cm, habitat use was restricted to the deep epibenthic zone. Small fish in the shallow epibenthic zone ate small and medium-sized prey (zooplankton, insect larvae and surface insects). Medium-sized fish in this zone were in addition feeding on the larger amphipod, *Pallasea quadrispinosa*. In the pelagic zone, the diet of medium-sized whitefish was dominated by zooplankton, although some larger prey like surface insects and age-0 smelt, *Osmerus eperlanus*, were also eaten. In the deep epibenthic zone, the diet of both medium-sized and large (< 35 cm) whitefish consisted mainly of the large prey *P. quadrispinosa*.

Introduction

Ontogenetic niche shifts have been shown to occur during the life of many fish species (Werner & Gilliam 1984, Persson 1990). As the fish grow, its habitat choice and diet change. Optimal prey size is generally positively correlated with fish size (Wankowski & Thorpe 1979), and diet shifts are often accompanied by relatively abrupt increases in food particle size or abundance of available prey (Larkin et al. 1957, Martin 1970, Werner 1979). Shifts to larger or more abundant prey may occur within one habitat, but are often associated with habitat shifts (Werner et al. 1981).

The optimal diet model predicts that the fish will select the prey that gives the highest net rate of energetic return (Mittelbach 1981, Stephens & Krebs 1986), modified by the relative predation risk in the various habitats available (Mittelbach 1984, Werner & Hall 1988). The risk of predation is

a major factor in habitat choice by small fish, but as fish size increases, predation risk decreases (Crowder & Cooper 1982, Werner et al. 1983). The optimal prey size, however, usually increases with increasing fish size.

Whitefish, *Coregonus lavaretus*, are omnivorous, and may feed on zooplankton, zoobenthos, surface insects and fish (Nilsson 1967, Svårdson 1976). As whitefish populations contain many size and age groups, we would expect this variability in diet to be associated with ontogenetic development. We would predict that the changes in diet and habitat use reflects the spatial variation in prey abundance and predation risk.

Whitefish in the deep, oligotrophic lake Mjøsa, Norway, are monomorphic, with a subterminal mouth and a mean gillraker number of 30 (Sandlund et al. 1987). Whitefish reach a body length of 12 cm during the first year and 20 cm during the second year. Asymptotic length was 31 cm. Fifty

percent sexual maturity was attained at age 5, at a mean length of 29 cm. Thus, post-maturity growth was low. However, a large proportion of the fish was old; more than 10% of the adults were older than 20 years. The whitefish stock is exploited only as a by-catch when fishing for other species.

In Mjøsa, food availability differs seasonally. Maximum abundance of the zoobenthos groups (insect larvae, molluscs, and oligochaetes) is found in July (Holtan et al. 1980). The amphipods *Pallasea quadrispinosa* and *Gammaracanthus loricatus* are also important zoobenthos, but, as they cannot be sampled quantitatively with an Ekman grab, their actual abundance is not known (Næsje et al. 1981). Maximum abundance of zooplankton is found in August/September, when the zooplankton community is dominated by *Daphnia galeata* and *Bosmina longispina* (Holtan et al. 1980, Kjellberg & Sandlund 1983).

Of the 20 fish species present in the lake, 3 are potential predators on whitefish older than a few weeks: piscivorous brown trout, *Salmo trutta*, in the pelagic zone; pike, *Esox lucius*, in littoral waters; and burbot, *Lota lota*, in profundal areas (Huitfeldt-Kaas 1917, Sandlund et al. 1985a, b).

Based on this, one might expect that benefits and costs for the whitefish should vary between habitats, and depend on the size of the fish. We therefore wanted to investigate the possible changes in habitat use of whitefish with increasing body size.

Methods

Study area

Mjøsa (61°30'N, 10°25'E, 121 m a.s.l.) is an oligo-mesotrophic, dimictic fjord lake in south-eastern Norway. Surface area is 365 km², maximum depth is 449 m, and mean depth is 153 m (Holtan 1979).

Sampling

Whitefish were sampled in Mjøsa from February to November 1979, by use of epibenthic and pelagic gill nets (Sandlund et al. 1985b). The gill nets con-

sisted of 12 panels (panel size, epibenthic: 25 × 2 m; pelagic: 25 × 6 m) with varying mesh sizes (8–52 mm bar mesh, mesh increments 2–7 mm). The pelagic nets were placed at the following depths: 0–10, 10–30, 30–50, and 50–90 m. The benthic nets were set from the shoreline down to 90 m. The exact depth of each net was recorded by an echo sounder (Simrad EL). The nets were fishing for 24 h, and catch per unit effort (CPUE) was calculated as number of fish per 100 m² net area for 24 hours fishing. A total of 806 whitefish between 17 and 46 cm in length were caught. Abundance of pelagic whitefish was estimated from data for fish density and relative size distribution collected with a Simrad EY-M echosounder (Lindem & Sandlund 1984).

Treatment of material

Fish were measured to the nearest 0.1 cm with the tail in a natural position and weighed to the nearest 1 g. Fish were 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 were estimated from undigested food items. The degree of diet similarity between size groups was calculated according to Schoener's (1968) similarity index

$$D = 1 - 1/2 \sum_{i=1}^n |p_i - q_i|, \text{ where } p_i \text{ is weight proportion of food item } i \text{ in population 1, } q_i \text{ is weight proportion of food item } i \text{ in population 2, and } n \text{ the number of food categories. } D \text{ varies between 0 and 1, representing no and complete food similarity, respectively.}$$

Results

Habitat

Catch per unit effort (CPUE) of whitefish in the epibenthic zone varied between 0.9 and 2.6, with a minimum during winter (Næsje et al. 1991). In the

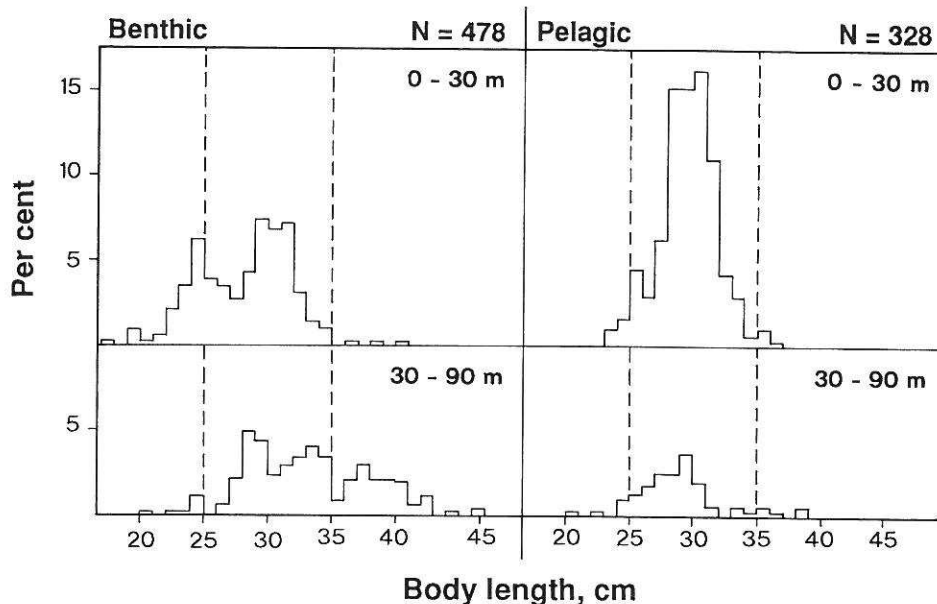


Fig. 1. Length distribution of whitefish caught in the epibenthic and pelagic habitat (depth zones 0–30 and 30–90 m) in Mjøsa, February–November 1979. N = number of fish in each habitat, all depths = 100%. Number of fish in the two depth zones were adjusted for catch effort.

pelagic zone whitefish catches were low from December through June (CPUE: 0.02–0.12), and high during August–October (CPUE: 0.40–2.09). A similar variation in the number of pelagic whitefish was also shown by hydroacoustic estimates, with the number of pelagic whitefish increasing from 24 fish ha^{-1} in May to a maximum of 182 fish ha^{-1} in September and decreasing to a minimum of 21 fish ha^{-1} in November (T. Lindem personal communication).

There was a partial habitat segregation between size groups of whitefish caught in gill nets (Fig. 1). Whitefish smaller than 25 cm in length were largely restricted to 0–30 m depth in the epibenthic zone. Fish between 25 and 35 cm in length were found from 0 to 90 m in the epibenthic zone and in the pelagic zone. In the pelagic zone, however, very few fish were caught deeper than 50 m. Fish larger than 35 cm in length were mainly found deeper than 30 m in the epibenthic zone. The difference in length distribution between depths in the epibenthic zone was highly significant ($X^2 = 209.4$, 2 d.f., $p < 0.005$). Furthermore, mean size of epibenthic whitefish increased significantly from the 0–30 m to

the 30–90 m depth zone (t-test, $p < 0.05$). In the pelagic zone length distributions between depths were also significantly different, due to relatively more small and large fish in the 30–90 m zone ($X^2 = 10.4$, 2 d.f., $p < 0.01$).

The partial habitat segregation between size groups concurs with segregation between age groups (Fig. 2). The 15–25 cm size group, living in the shallow epibenthic zone, consisted of fish younger than 6 years, with a mean age of 2.3 years. The 25–35 cm size group, which was living in all three habitats, included fish of ages from 2 to more than 20 years. Within this size group there was a significant difference in age distribution between the pelagic and shallow epibenthic habitat ($X^2 = 20.9$, 3 d.f., $p < 0.005$), although mean ages in the two habitats were not significantly different (10.2 vs. 8.8 years, t-test, $p > 0.05$). There was a significantly larger proportion of old fish among 25–35 cm fish in the deep epibenthic habitat than in the shallow epibenthic habitat ($X^2 = 74.6$, 3 d.f., $p < 0.005$). This is also reflected in the significantly higher mean age in the deep epibenthic habitat than in the shallow epibenthic and pelagic habitats

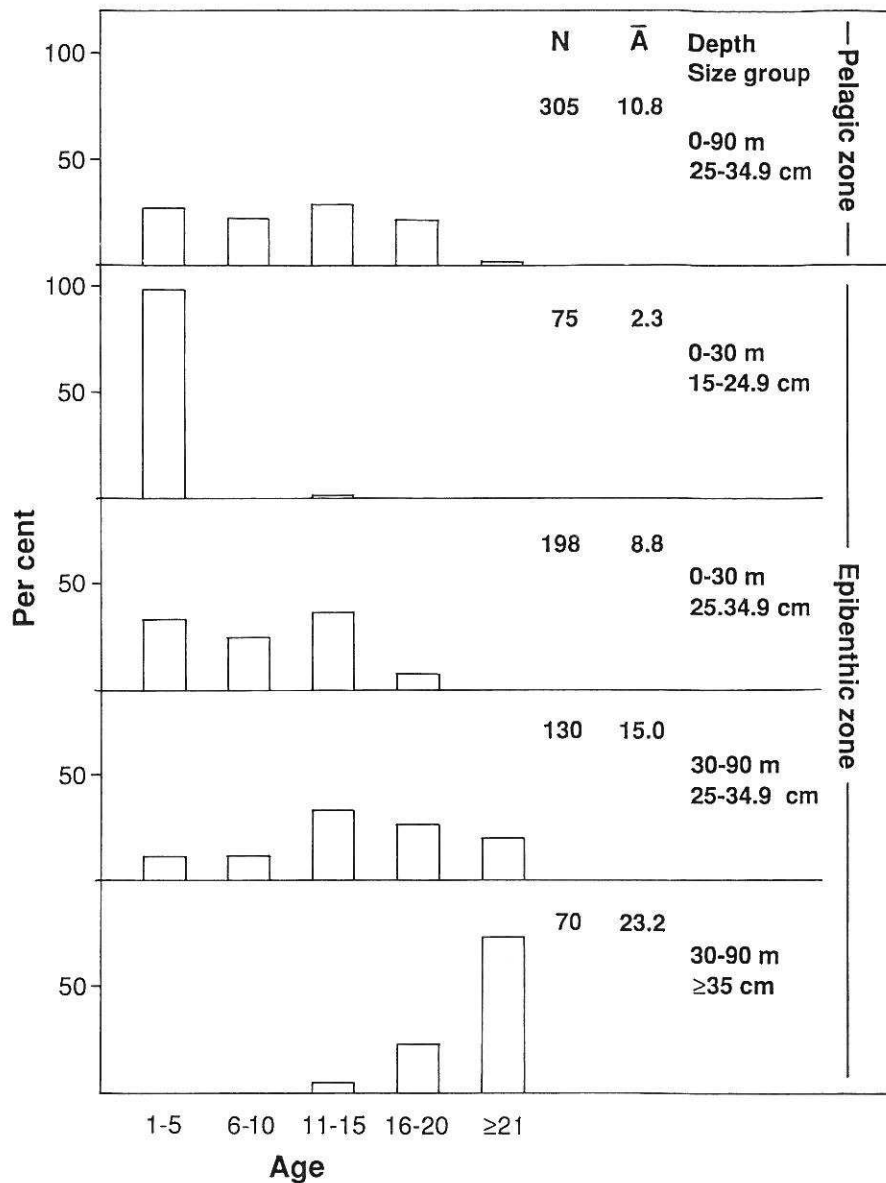


Fig. 2. Age distribution of the various size groups of whitefish caught in the pelagic zone (0–90 m) and in the shallow (0–30 m) and deep (30–90 m) epibenthic zone in Mjøsa, February–November 1979. N = number of fish. A = mean age (years) in sample.

(15.0 vs. 8.8 and 10.2 years, respectively, t-tests, $p < 0.05$). There was no significant difference in age distribution between 25–34.9 cm pelagic whitefish and the pooled material of this length group from the epibenthic habitat (0–90 m) ($X^2 = 3.66$, 3 d.f., $p > 0.05$). Mean age of fish larger than 35 cm, restricted to the deep epibenthic zone, was 23.2 years.

Diet

The prey taken by whitefish may be grouped according to their wet weight into three size classes (Table 1). Small prey (<1 mg wet weight) are crustacean zooplankton, mainly within a pelagic habitat, although they may also be found close to the substratum. Medium sized prey (1–5.9 mg wet weight) are large cladoceran zooplankton, mol-

luses, insect larvae and pupae, and surface insects. Thus, this prey size is found in all habitats. Among large prey (≥ 6 mg wet weight), the benthic amphipod *P. quadrispinosa* was important whitefish food, whereas *Mysis relicta* and age-0 smelt, *Osmerus eperlanus*, were eaten occasionally.

In the epibenthic zone, there was a segregation in diet between whitefish caught in the 0–30 m depth zone and in deeper waters (Fig. 3). In the 0–30 m depth zone, all size groups had a varied diet, dominated by small and medium sized prey (cladocerans and chironomid larvae, cf. Table 1). Deeper than 30 m the diet of 25–35 cm fish and fish > 35 cm was nearly identical, as both groups depended heavily on *P. quadrispinosa*. The similarity in diet between the size groups in deep waters is indicated by the high diet overlap (Schoener's $D = 0.913$ – 0.997 ; Fig. 4) which was significantly higher (Wilcoxon's rank test, $p < 0.01$) than the corresponding indices of diet overlap between 15–25 cm and 25–35 cm fish in shallow waters (0.337 – 0.789).

Table 1. Wet weights of prey in subadult and adult whitefish stomachs, Lake Mjøsa 1979 (approximate means, over all months). Only prey groups constituting more than 1% wet weight of stomach contents at any time are included. Habitat (P = pelagic, SB = epibenthic 0–30 m, DB = epibenthic 30–90 m) indicates where this prey was important food.

Taxon	Average wet weight (mg)	Habitat
Weight group < 1 mg		
<i>Bosmina longispina</i>	0.04	P, SB
<i>Daphnia galeata</i>	0.12	P, SB
<i>Cyclops lacustris</i>	0.12	P, SB
<i>Eudiaptomus gracilis</i>	0.05	P, SB
<i>Limnocalanus macrurus</i>	0.24	P, SB
Weight group 1–5.9 mg		
<i>Leptodora kindtii</i>	2.0	P, SB
<i>Bythotrephes longimanus</i>	2.0	P, SB
Chironomidae larvae	1.7	SB
Chironomidae pupae	1.7	SB
Trichoptera larvae	5.4	SB
<i>Pisidium</i> spp.	1.7	SB, DB
<i>Gyraulus</i> spp.	3.7	SB
Surface insects	3.0	P, SB
Weight group ≥ 6 mg		
<i>Pallasea quadrispinosa</i>	16.8	SB, DB
<i>Mysis relicta</i>	8.0	SB
Fish (age-0 smelt)	90.0	P

In the epibenthic habitat, the frequency of fish with large prey (≥ 6 mg wet weight) in the stomachs increased with increasing fish size (Wilcoxon-tests, $p < 0.01$; Fig. 5).

In the pelagic zone there was no significant difference in diet between fish caught in various depth zones, and they were therefore pooled. Pelagic whitefish had eaten essentially the same proportion of size groups of prey as the smaller fish in the shallow epibenthic habitat (Fig. 3). The frequency of pelagic 25–35 cm fish that had eaten large prey (≥ 6 mg wet weight) was significantly lower than among fish of the same size, and similar to the frequency among smaller fish (15–25 cm), in the epibenthic zone (Wilcoxon-tests, $p < 0.01$ and $p > 0.05$, respectively; Fig. 5).

Discussion

Our data demonstrate two changes in habitat use during the life span of whitefish in Mjøsa. When the fish reach a body length of approximately 25 cm, their habitat is expanded from the shallow (0–30 m) epibenthic zone to include all three main habitats; the shallow and the deep (30–90 m) epibenthic zone as well as the pelagic zone. At the same time, the diet is diversified to include zooplankton in the pelagic zone and *P. quadrispinosa* in the deep epibenthic zone.

The second ontogenetic change in habitat use occurs when the whitefish reach a body length of approximately 35 cm. From this size, their habitat is confined to the deep epibenthic zone, and the diet is chiefly restricted to *P. quadrispinosa*.

Ontogenetic habitat shifts in animals are the results of trade-offs between feeding (growth rate) and predation risks (mortality) (Stamps 1983, Power 1984, Gilliam & Fraser 1987, Werner & Hall 1988). In the absence of predation risk, as in large-sized fish, the shifts between habitats should be determined by prey available, and energy spent on search, capture and handling of prey (Werner & Hall 1974, Abrahams & Dill 1989).

The juvenile whitefish in Mjøsa stay in the littoral zone from the time of metamorphosis, and start feeding as larvae at a length of 16 mm (Næsje et al.

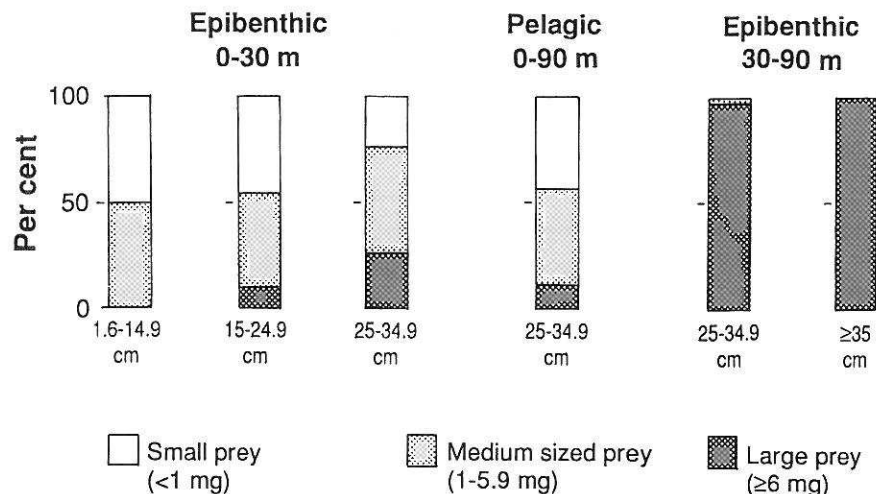


Fig. 3. Diet of whitefish in the epibenthic habitat (depth zones 0–30 m and 30–90 m) and in the pelagic habitat (0–90 m); mean over the sampling periods February–November 1979, in Mjøsa. Sample sizes: Epibenthic 0–30 m, <15 cm: 59 fish; 15–24.9 cm: 39 fish; 25–34.9 cm: 138 fish. Pelagic 0–90 m: 247 fish. Epibenthic 30–90 m, 25–34.9 cm: 87 fish; >= 35 cm: 69 fish. Data for fish ≤ 14.9 cm from Næsje et al. (1986).

1986). This is the habitat which the most abundant zoobenthos (Holtan et al. 1980), but the availability of benthic prey may be low, due to interspecific competition, as most other fish species in the lake also live in the littoral zone (Sandlund et al. 1985b). A part of the stock of medium-sized whitefish exploit pelagic waters during late summer and autumn, and the offshore movement is significantly correlated with the abundance of zooplankton (Næsje et al. 1991). This accords with the pre-

diction that parts of the stock should change habitat when the food situation improves offshore. However, we do not know whether the relative distribution of medium-sized whitefish is in proportion to the abundance of food resources in the various habitats (the ideal free distribution model; Fretwell & Lucas 1970). From a fish-size/prey-size consideration, we would expect zooplankton to be a more profitable prey for small whitefish (Wankowski & Thorpe 1979), but the smaller whitefish may stay

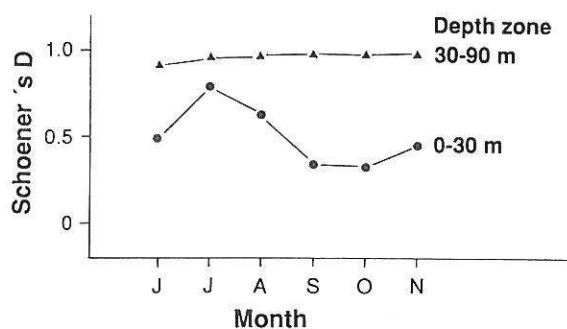


Fig. 4. Schoener's (1968) diet overlap index (D) between whitefish length groups in the epibenthic habitat in Mjøsa: 0–30 m depth zone: between 15–24.9 cm and 25–34.9 cm length groups, 30–90 m depth zone: 25–34.9 cm and >= 35 cm length groups. Sample sizes as in Fig. 3.

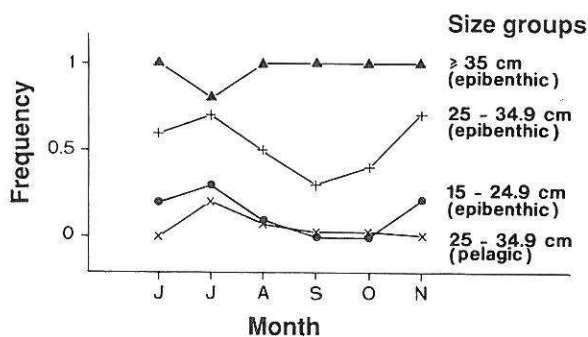


Fig. 5. Frequency of occurrence of large prey (≥6 mg wet weight, cf. Table 1) in the stomachs of the various size groups of whitefish in L. Mjøsa. Fish ≤ 14.9 cm had eaten no large prey (cf. Fig. 3).

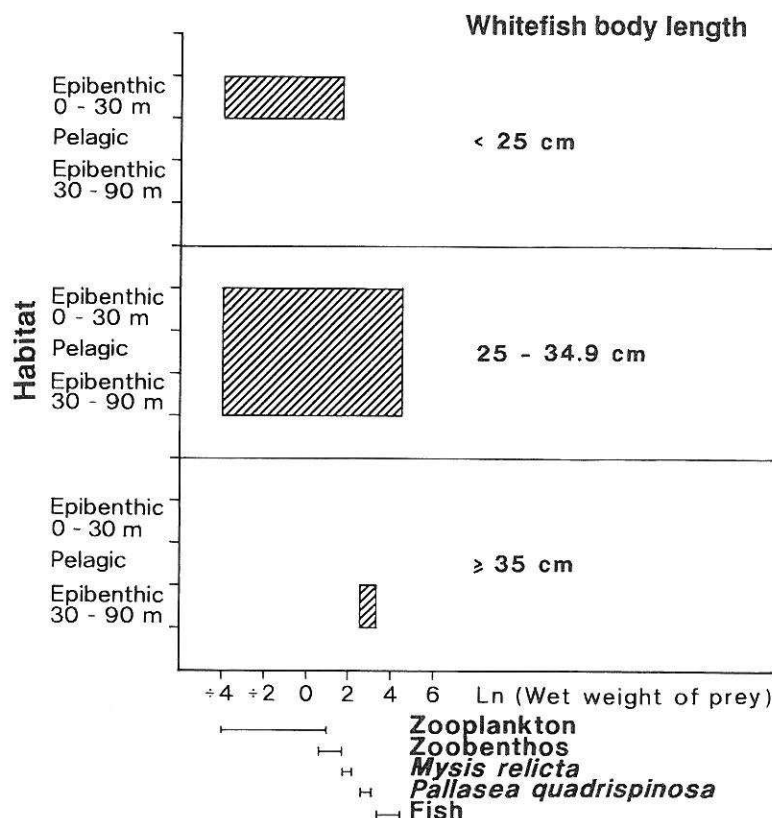


Fig. 6. Summary of ontogenetic niche shifts (in terms of prey size and habitat) in whitefish in L. Mjøsa. Sizes of prey in some prey groups of importance for whitefish is indicated below the horizontal axis. Three habitats are defined within the lake (vertical axis). Based on present data and Næsje et al. (1986).

close to the bottom because it is safer to dwell in a structured habitat than moving offshore (Crowder & Cooper 1982).

In the pelagic zone, brown trout and the occasional large pike are potential predators on whitefish. Brown trout in Mjøsa eats mainly smelt, which is usually less than 15 cm in length. Only 4% of the prey fishes in the stomachs of 75 predatory brown trout were larger than 15 cm (Taugbøl et al. 1989). Small pike (< 60 cm) in Mjøsa tend to stay in shallow protected bays where there is some macrovegetation. Larger pike tend also to move in the exposed littoral areas, and are occasionally caught in the pelagic zone (Sandlund et al. 1985b). Little is known about the diet of pike in Mjøsa, but in the Norwegian lake Tyrifjorden, with a similar fish community, only large pike (> 60 cm) to some extent ate adult whitefish (≈ 30 cm) (Vøllestad et al. 1986). The third potential predator in Mjøsa,

burbot, live mainly in the deep epibenthic zone, and feeds on smelt (Sandlund et al. 1985a). The apparent concentration of prey sizes below 15 cm is probably due to this being the adult size of smelt, which seems to be the most easily available prey species. Even so, for whitefish predation risk will probably decrease quite quickly as they approach adult size.

The change in habitat use by whitefish at the size of 25 cm might be termed an expansion of the niche (Fig. 6). Whitefish between 25 and 35 cm utilize all main habitats, including the shallow benthic zone used by smaller fish and the deep benthic zone used by larger fish, and a wide spectrum of prey sizes. Individuals moving into the deeper benthic zone find larger prey (*P. quadrispinosa*). However, because the whitefish is a visual predator (Braum 1978), searching time may be longer in darkness. Feeding in the pelagic zone involves utilizing small-

er prey, but at high zooplankton densities searching and handling time is short (Werner & Hall 1974).

The asymptotic length of the Mjøsa whitefish is 31 cm. Thus, relatively few fish ever reach the > 35 cm length group. We may hypothesize that the post-maturity growth necessary to become larger than 35 cm may depend on a diet shift from small and medium-sized prey to the large *P. quadrispinosa*, giving a larger energy surplus. In bluegills, *Lepomis macrochira*, Mittelbach (1983) demonstrated that the fish ceased growing if the availability of large prey was low.

Broadly speaking, the whitefish stock thus consists of three ecologically functional units: small littoral fish, medium-sized fish utilizing all habitats, and large profundal fish. These ecological units each include a high number of age groups. Medium-sized fish include more than 20 age groups, whereas large fish include from age 12 upwards. Age distribution in the two groups overlap to a large extent, indicating that the whitefish population is size-structured rather than age-structured (Ebenman & Persson 1988).

Acknowledgements

We want to thank Leif Gjestad, Helge Hagen, Gerd Justås, and Gösta Kjellberg for assistance during field work, and Torfinn Lindem for providing hydroacoustic data. Tom G. Northcote provided constructive comments on the manuscript.

References cited

- Abrahams, M.V. & L.M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70: 999–1007.
- Braum, E. 1978. Ecological aspects of the survival of fish eggs, embryos and larvae. pp. 102–131. *In*: S.D. Gerking (ed.) *Ecology of freshwater fish production*, Blackwell Scientific Publications, Oxford.
- Christensen, J.M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. *J. Cons. Int. Explor. Mer.* 29: 73–81.
- Crowder, L.B. & W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63: 1802–1813.
- Ebenman, B. & L. Persson (ed.). 1988. Size-structured populations. *Ecology and evolution*. Springer-Verlag, Berlin. 284 pp.
- Fretwell, S.L. & H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 315–357.
- Gilliam, J.F. & D.F. Fraser 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68: 1856–1862.
- Holtan, H. 1979. The Lake Mjøsa story. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 13: 242–258.
- Holtan, H., G. Kjellberg & P. Brettum. 1980. Monitoring of Lake Mjøsa. Progress report 10. Investigations in 1979. Norwegian Institute of Water Research Report 0-79079: 1–212. (In Norwegian.)
- Huitfeldt-Kaas, H. 1917. The fish & fisheries of Lake Mjøsa. *Det Kgl. Norske Videnskabers Selskap, Skrifter* 2: 1–257. (In Norwegian.)
- Kjellberg, G. & O.T. Sandlund. 1983. Trophic relationships in the pelagic zone of Lake Mjøsa. *Direktoratet for vilt og ferskvannsfisk, Mjøsundersøkelsen, Report* 6: 1–61. (In Norwegian.)
- Larkin, P.A., J.G. Terpenning & R.R. Parker. 1957. Size as a determinant of growth rate in rainbow trout *Salmo gairdneri*. *Trans. Amer. Fish. Soc.* 86: 84–96.
- Lindem, T. & O.T. Sandlund. 1984. New methods in assessment of pelagic freshwater fish stocks – coordinated use of echosounder, pelagic trawl and pelagic nets. *Fauna (Oslo)* 37: 105–111. (In Norwegian.)
- Martin, N.W. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. *J. Fish. Res. Board Can.* 27: 125–146.
- Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegill. *Ecology* 62: 1370–1386.
- Mittelbach, G.G. 1983. Optimal foraging and growth in bluegills. *Oecologia* 59: 157–162.
- Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* 65: 499–515.
- Næsje, T.F., B. Jonsson, O.T. Sandlund & G. Kjellberg. 1991. Habitat switch and niche overlap in coregonids: effects of zooplankton abundance. *Can. J. Fish. Aquat. Sci.* (in press).
- Næsje, T.F., O.T. Sandlund & B. Jonsson. 1986. Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*. *Env. Biol. Fish.* 15: 309–314.
- Næsje, T.F., O.T. Sandlund, L. Klyve & H. Hagen. 1981. The amphipode *Gammaracanthus loricatus* var. *lacustris* in Lake Mjøsa. *Fauna (Oslo)* 34: 44–45. (In Norwegian.)
- Nilsson, N.-A. 1967. Interactive segregation between fish species. pp. 295–313. *In*: S.D. Gerking (ed.) *Biological Basis of Freshwater Fish Production*, Blackwell Scientific Publications, Oxford.
- Persson, L. 1990. Predicting ontogenetic niche shifts in the field: what can be gained by foraging theory? pp. 303–321. *In*: R.N.

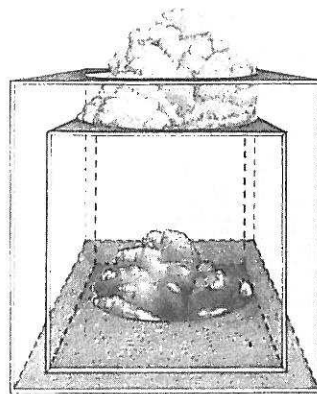
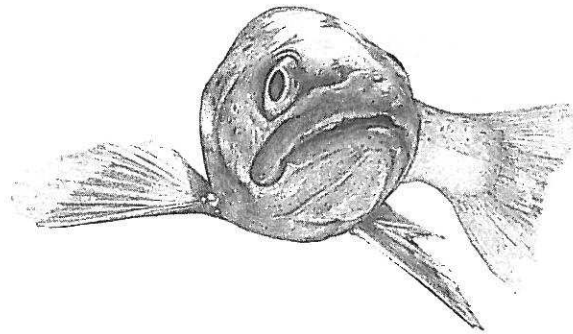
- Hughes (ed.) Behavioural Mechanisms of Food Selection, Springer-Verlag, Berlin.
- Power, M.E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? *Ecology* 65: 523–528.
- Sandlund, O.T., L. Klyve & T.F. Næsje. 1985a. Growth, habitat and food of burbot *Lota lota* in Lake Mjøsa. *Fauna (Oslo)* 38: 37–43. (In Norwegian.)
- Sandlund, O.T., T.F. Næsje, L. Klyve & T. Lindem. 1985b. The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill-net catches and echo sounder. *Rep. Inst. Freshwat. Res. Drottningholm* 62: 136–149.
- Sandlund, O.T., T.F. Næsje & G. Kjellberg. 1987. The size selection of *Bosmina longispina* and *Daphnia galeata* by co-occurring cisco (*Coregonus albula*), whitefish (*C. lavaretus*) and smelt (*Osmerus eperlanus*). *Arch. Hydrobiol.* 110: 357–363.
- Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726.
- Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behav. Ecol. Sociobiol.* 12: 19–33.
- Stephens, D.W. & J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton. 247 pp.
- Svårdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. *Rep. Inst. Freshwat. Res. Drottningholm* 55: 144–171.
- Taugbøl, T., O. Hegge, T. Qvenild & J. Skurdal. 1989. The diet of brown trout in Lake Mjøsa. Fylkesmannen i Oppland, Miljøvernveddelingen. Report 15: 1–17. (In Norwegian.)
- Vøllestad, L.A., J. Skurdal & T. Qvenild. 1986. Habitat use, growth, and feeding of pike (*Esox lucius* L.) in four Norwegian lakes. *Arch. Hydrobiol.* 108: 107–117.
- Wankowski, J.W.J. & J.E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* 14: 351–370.
- Werner, E.E. 1979. Niche partitioning by food size in fish communities. pp. 311–322. *In*: H. Clepper (ed.) *Predator-Prey Systems in Fisheries Management*, Sport Fishing Institute, Washington.
- Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15: 393–425.
- Werner, E.E., J.F. Gilliam, D.J. Hall & G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540–1548.
- Werner, E.E. & D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55: 1042–1052.
- Werner, E.E. & D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69: 1352–1366.
- Werner, E.E., G.G. Mittelbach & D.J. Hall. 1981. Foraging profitability and the role of experience in habitat use by the bluegill sunfish. *Ecology* 62: 116–125.

Fish imagery in art 15: Ikegawa's untitled pencil drawing

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Shiro Ikegawa (b. 1933) is a Los Angeles artist whose work combines Japanese and American traditions. His original training in art took place in Japan and focused on Western techniques. In 1950 he emigrated to the United States to pursue his interest in abstract expressionism; he became widely known for his three dimensional prints. In 1965 he returned briefly to Japan seeking his cultural roots but he was shocked by the environmental and spiritual degradation he observed. Ikegawa eventually found the serenity he sought in the mountains of California. He became intrigued by the trout he caught and observed in streams there and began including them in his art, exploring what it is like to *be* a fish suspended in the water. In the untitled drawing below, the trout is suspended above the clouds, creating a feeling for the weightlessness fish experience. The blank space around the drawn images gives the work a strongly Oriental cast, yet the fish stares out at the viewer in a distinctly Western manner. The variety of works Ikegawa has produced using trout is impressive, from prints of various types, to ceramic fish-on-platters, to drawings and collages that would not be out of place in an ichthyology text.



The drawing (80 × 57 cm) is used courtesy of the artist.