Nocturnal Foraging by Alewives in Reservoir Coves

William E. Kelso, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061*

John J. Ney, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061*

Abstract: Diel occurrence and feeding of alewives (*Alosa pseudoharengus*) in shoreline areas of Claytor Lake, Virginia was investigated concurrent with food habits of resident juvenile bluegill (*Lepomis macrochirus*), pumpkinseed (*L. gibbosus*), and yellow perch (*Perca flavescens*); and the composition and abundance of the littoral zooplankton community. Schools of alewives entered coves at sunset and fed intensively through the night, departing soon after sunrise. Alewives and juvenile fish consumed the same 16 items, but to different degrees. Alewives fed primarily on zooplankton in the water column, whereas the juvenile fish ate mostly epibenthic forms with which they were associated in the aquatic macrophyte/brush habitat. Alewife stomachs contained 9 to 30 times the volume and number of items as did those of juvenile fish. The high foraging efficiency of alewives in large schools may result in trophic competition with littoral zooplanktivores despite partial resource partitioning.

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The landlocked alewife is currently a popular candidate for introduction into lake and reservoirs as a pelagic forage fish. Interest has been stimulated by the development of highly successful salmonid fisheries in the Great Lakes which depend on alewife as the principal forage. The introduction of any forage species presents both benefits and risks to the resident fish community (Ney 1981). The suitability of the alewife as a pelagic forage fish for inland waters has been assessed on the basis of its performance in the Great Lakes, New England lakes, and a mainstream Virginia reservoir, Claytor Lake (Kohler and Ney 1981a, Ney et al. 1982). Positive attributes include prolificacy, resilience, and high utilization by pelagic piscivores. On the negative side, alewives can be occasional piscivores (Kohler and Ney 1980) as well as highly selective zooplanktivores; both predation and trophic competition by alewives have been cited as probable causes for the collapse of native fish populations in the Great Lakes concurrent with alewife establishment (Smith 1970, Wells and McLain 1972, Crowder 1980).

Competition with planktivorous species or life stages is potentially the more pervasive and enduring interspecific impact. Alewives are such efficient size-selective planktivores that they have altered the size and species composition of the zooplankton community in every lake where the alewife-zooplankton relationship has been investigated (Brooks and Dodson 1965, Wells 1970, Hutchinson 1971, Warshaw 1972, Kohler and Ney 1981b). However, direct proof of trophic competition is lacking, perhaps in large measure due to the difficulty of establishing a shortage of the zooplankton resource. In warmwater southeastern storage reservoirs, interspecific trophic competition may be minimized if alewives feed only in the pelagic region. The principal resident zooplanktivores in these systems are larval and juvenile stages of sport fish species, which are largely shore-oriented. Trophic overlap between alewife and young-of-the-year sport fish species in Claytor Lake has been observed to be low (Kohler and Ney 1981a), although comparisons were biased because larval fish and alewife collections did not coincide in either time or space.

However, we have frequently observed large schools of alewives moving into the shallow coves of Claytor Lake in the evening. If feeding, these schools could exert a direct impact on the food supply of young sport fishes. In this paper, we describe inshore feeding by alewives and consider its significance as related to the food habits and trophic resource of juvenile bluegill, pumpkinseed, and yellow perch.

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Methods

Claytor Lake is a 1,820 ha mainstream impoundment of the New River in southwestern Virginia. Its shallow (<5 m depth) coves grade steeply into the 26 km long main channel. The fish community of this marginally eutrophic reservoir is comparable to other southeastern impoundments, featuring black bass (*Micropterus* sp.) and other centrarchids as well as channel catfish (*Ictalurus punctatus*), walleye (*Stizostedion vitreum*), white bass (*Morone chrysops*), and striped bass (*M. saxatilis*). Physical-chemical features of Claytor Lake and the fish community have been described in detail by

Kohler and Ney (1981a,b). Alewives were introduced in 1968 from a landlocked New Jersey stock and soon established a large population (Boaze 1972).

Alewives and juvenile sport fish were collected from 3 coves approximately 1, 4, and 7 km upstream of the Claytor Lake dam between 7 July and 2 September 1980. Collections were made in each cove at 1- to 2-week intervals with a boat-mounted DC electrofishing unit. Only areas 0–2 m deep were sampled since juvenile fishes were associated primarily with the aquatic macrophyte-brush habitat of the shoreline area. Bluegill, pumpkinseed, and yellow perch were the most abundant juvenile fishes (ages 0 and 1) consistently captured in the coves during the July–August period, and analysis of food habits was restricted to these species. Collections in each cove were spaced 2–4 hours apart on every sampling date. Sampling times were rotated on successive dates so that collections were made over the entire 24-hour cycle in each cove. Upon capture, fish were killed and placed in 10% formalin, then transferred to 40% isopropanol within 2 weeks.

Zooplankton was sampled in each cove on each fish collection date by 2 complimentary methods. Zooplankton in the water column was obtained with 3 vertical tows of a 0.3-m dia., 63-μ mesh plankton net. Epibenthic zooplankters, defined here as microcrustaceans which are associated with the bottom or the submerged aquatic macrophyte and brush structure characteristic of cove shorelines in Claytor Lake, were taken with a 1296-cm^2 pattern sampler (Whiteside and Williams 1976) set overnight. The pattern sampler consisted of a tray of inverted funnels attached to glass jars which trapped the epibenthic zooplankters as they migrated vertically during the night. Zooplankton samples were preserved in the field with 70% isopropanol—3% formalin. Density estimates for zooplankton were made by combining counts from net tows and the pattern sampler on a number/l basis.

In the laboratory, zooplankton samples and stomach contents of fish were placed in vials and allowed to settle. Dense zooplankton collections were subsampled to 1/8 or 1/16 of original concentration. Organisms were pipetted onto glass slides and stained and mounted in commercially available media (CMCP 9AF & 10, Masters Chemical Company). All organisms from each fish stomach and zooplankton sample were identified and enumerated except that 2 replicate subsamples were used for zooplankton description when concentrations were very high. A random subsample of 40 organisms/taxon (as available) on each slide was measured for total length. Stomach contents of fish were analyzed by standard frequency-of-occurrence and volumetric methods (Lagler 1956, Windell and Bowen 1978). Volumes of diet items were calculated indirectly by geometric approximation (Kutkuhn 1958, McComish 1967). A stomach fullness index (SFI) was calculated for alewives to assess time of feeding. The 3 greatest absolute stomach volumes in each of the 2 alewife length classes (60–80 mm and 145–185 mm total length) were averaged and designated as 100% full; individual stomach volumes were then divided by this value to obtain the SFI percentage. SFI will provide a biased estimate of feeding chronology if ingestion and evacuation rates differ (Eggers 1977). However, bias will be minimized if ingestion rates change sharply during the diel cycle and if evacuation is rapid. At summer water temperatures (>20 C), zooplankton are evacuated from alewife stomachs within 2–4 hours (Gannon 1976).

Results

Alewives demonstrated a striking periodicity of occurrence in the littoral areas of Claytor Lake. Sporadic diurnal movements into shallow areas were seen occasionally, though alewives were usually absent from the coves during daylight hours. In crepuscular periods, however, movement inshore increased dramatically, and alewives remained in the coves throughout the night (Fig. 1a). As dawn approached, a reverse migration took place; almost all alewives were gone from the coves within 1 hour after sunrise. In addition to alewives electroshocked along the shoreline (N = 68), large schools were readily seen in the open water of the coves by spotlight.

Analysis of alewife stomach fullness demonstrated that alewives fed heavily during their nocturnal migrations (Fig. 1b). Feeding intensity appeared to be greatest at sunset but persisted through the night. Examination of stomach contents indicated that much, if not most of the nocturnal feeding by migrating schools occurred in littoral areas. Epibenthic organisms, found almost exclusively in the littoral area, were commonly consumed (Table 1). Copepods in alewife stomachs were predominately *Mesocyclops edax,* a large cyclopoid copepod not found in the limnetic regions of Claytor Lake (Kohler 1980). Conversely, *Diaptomus reighardi,* a calanoid copepod often consumed by alewives in the limnetic regions, was not found in any cove-captured alewives. Of the 2 species of *Diaphanosoma* in Claytor Lake, the limnetic form, *D. leuctenbergianum,* was absent from these alewife stomachs but the littoral form *D. brachyurum* was frequently encountered.

Diets of alewives and the juvenile cove fishes showed complete qualitative overlap; all 16 items were found in 1 or more stomachs of each fish species (Table 1, Fig. 1). Approximately 60% of alewife stomach contents by volume consisted of strictly littoral microcrustaceans and insects. These items collectively represented 66%, 72%, and 93% by volume of the stomach contents of juvenile yellow perch, bluegill, and pumpkinseeds, respectively. Significant differences ($P \leq 0.05$, Student's t-test) between alewives and any of the other species in mean size of food items were rare and inconsistent (Table 1).

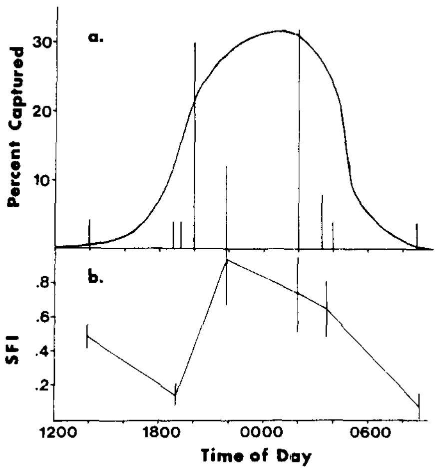

Figure 1. Diel variation in occurrence (a.) and stomach fullness (b.) of alewives captured in coves of Claytor Lake.

However, when the percentage volume compositions of diets are compared (Fig. 2), it is obvious that the relative importance of particular items differed markedly for alewifes versus juvenile sunfishes and yellow perch. Alewives fed predominately on planktonic forms, especially copepods and the cladocerans, *Bosmina longirostris* and *Diaphanosoma brachyurum.* In contrast, juvenile fish fed principally on epibenthic organisms; only *Bosmina* among planktonic forms was a major item for any of the juvenile fish, contributing averages of 12% and 23% to the diet volumes of yellow perch and bluegills, respectively. Ranking of the importance of items in the diet by percentage volume contribution showed no significant correlations between alewife and any of the 3 cove species ($P > 0.5$, Spearman's rank correlation).

Alewives were much more voracious feeders than the juvenile sunfishes and yellow perch. Stomach volumes averaged 9 to 30 times greater for alewives than for any of the other species. Differences in volume were reflected in numbers of items per stomach as well (Table 1). Alewives contained many timse more *Bosmina, Diaphanosoma,* and copepods than did the juvenile fishes. However, only ostracods and *Chydorus* among the epibenthic items occurred in greater number in alewife stomachs. Ranking of food item importance by number also showed no significant correlations between alewife and any of the cove species ($P > 0.3$, Spearman's rank correlation).

Table 1. Average Available Food Item Densities and Numerical Abundances in Fish Diets

Food Items	Mean Water Column Densities (Number/l)	Number of Items/Stomach			
		Alewife	Bluegill	Pumpkinseed	Yellow Perch
Planktonic Items					
Bosmina longirostris	29.11	629.1	107.2	1.4[b]	103.4
Copepods	9.44	23.4	4.0	4.5	2.1
Ceriodaphnia quadrangula	0.25	1.1	3.9[a]	0.1	2.0[b]
Diaphanosoma brachyurum	1.03	337.3	1.3	0.1	0.2[b]
Dipteran pupae	0.04	0.8	0.1	0.2	0.5
Structure Oriented Items					
Alona	0.52	0.9	2.1	2.7	1.3
Amphipoda	0.02	0.1	0.2	0.1	0.6
Camptocercus rectirostris	0.22	0.2	2.0	0.6	1.0
Chydorus sphaericus	0.30	9.8	4.9	0.5	0.5[b]
Dipteran larvae	0.05	0.2	3.0	6.5	4.6
Eurycercus lamellatus	0.09	0.2	2.1	0.8	5.0
Hydracarina	0.44	0.4	0.4	1.5	0.2
Ostracoda	3.26	2.4	7.1	0.9	1.6[a]
Pleuroxus	0.01	0.1	1.4[a]	0.4[a]	0.1
Latona setifera + *Sida crystallina*	0.31	0.1	8.7	1.4	16.3
Simocephalus expinosus	0.01	0.1	1.0	0.2	0.5
Number of Fish/Empty Stomachs		68/14	96/22	62/20	34/8
Mean Total Length (mm)		88.7	61.4	68.2	119.2
Mean Number of Prey per Stomach		1,006	150	22	140
Mean Volume of Prey per Stomach (mm^3)		128.4	6.6	4.2	13.2

[a] Mean length significantly ($P < 0.05$) larger in alewives.
[b] Mean length significantly ($P < 0.05$) smaller in alewives.

Discussion

Nocturnal inshore migrations by alewives have previously been related to spawning activity (Nigro and Ney 1982), but our findings demonstrate that inshore foraging migrations also occur. Spawning activity is characterized by loud and frequent surface splashing (Edsall 1964), whereas the schools we encountered only occasionally "dimpled" the water surface. Alewives commonly feed at night in limnetic waters (Janssen and Brandt 1980, Kohler and Ney 1980), although the importance of night feeding to the total diet has not been assessed. Our data, if representative, would indicate that the major feeding period is nocturnal, but few alewives were captured in coves during daylight hours. Nocturnal inshore feeding migrations may have adaptive value in simultaneously optimizing prey availability and predator avoidance. Littoral zooplankton migrate vertically into the water column at night from benthic cover. Conversely, littoral piscivores are day active; stomachs of black basses in Claytor Lake rarely contained alewives (Kohler and Ney 1981a). Hall et al. (1979) reported a comparable but reverse feeding migration of golden shiners (*Notemigonus crysoleucas*) offshore at night in a small Michigan lake. The golden shiners exploited the nocturnal vertical migrations of limnetic *Daphnia.* Although the authors attributed the movement to trophic competition with littoral centrarchids, it may also have had adaptive value in avoidance of the day-active piscivores of the lake because littoral macrophyte beds provided protective cover. In contrast, pelagic piscivores in Claytor Lake (white bass, striped bass, walleye) feed readily at night.

The impact of nocturnal foraging by alewives on the food supply of planktivorous cove fishes is difficult to assess. Habitat and temporal partitioning between alewives and juvenile sunfishes and perch appears to mitigate direct competition. Alewives fed in the coves at night, whereas the juvenile cove fishes feed during the day. Alewives also consumed primarily planktonic species which occurred in the water column. The bulk of the diet of the juvenile planktivores consisted of epibenthic species which cohabited the aquatic macrophyte-brush habitat of the shoreline area with these fish. The high frequency of occurrence but low relative volume of epibenthic forms in alewife stomachs indicate that epibenthic zooplankters may be consumed as encountered when they rise into the water column during the night; alewives do not feed effectively on benthic prey (Janssen 1978). In this situation, the impact of alewife nocturnal foraging on epibenthic zooplankton populations would depend on the timing, duration, and extent of the vertical migrations of each species (Redfield and Goldman 1980, Fairchild 1981).

However, alewives are extremely efficient feeders and undeniably reduce the food supply of both planktonic and epibenthic items available to cove residents. In Claytor Lake, growth in the first years of life has declined in the last 30 years for at least several species which reside in littoral areas through the juvenile stage (Ney et al. 1982). Because of the many perturbations which typically affect the fish community in an ageing reservoir, these declines cannot be attributed to trophic competition with alewives. They do, however, raise concern, especially in consideration of the high densities of alewife schools, the duration and intensity of their nocturnal foraging, and their efficiency as zooplanktivores.

A definitive assessment of trophic interactions of alewives and littoral zooplanktivores will require both temporal (before and after) and spatial (with and without alewives) comparisons of the trophic resources of coves and the feeding ecology, abundance, and growth of cove fishes. An appropriate experimental design can be developed for systems where alewives now occur by manipulating their access to coves. Alternatively, but less desirably, before-and-after studies should be conducted in systems for which alewife

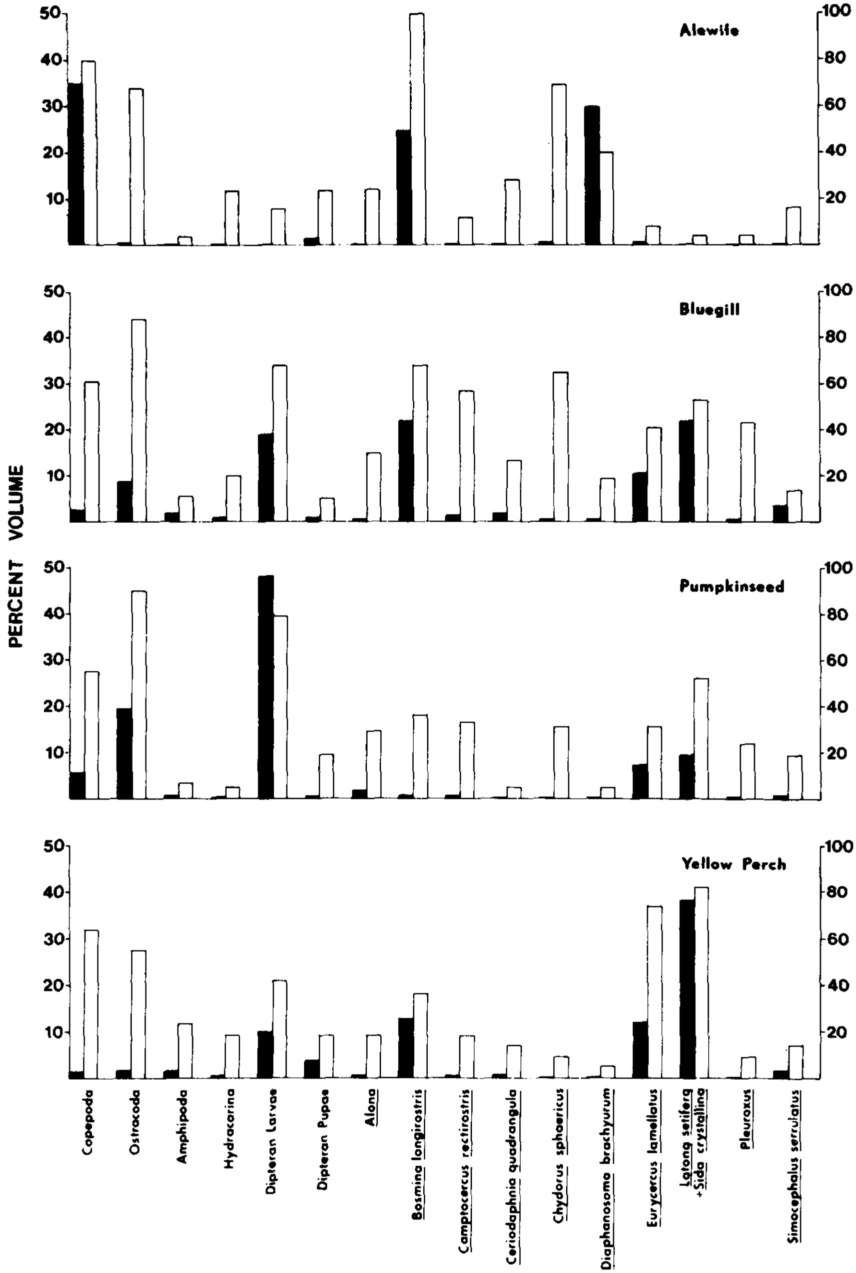

Figure 2. Composition of stomach contents of alewives and juvenile fishes captured in Claytor Lake coves. Shaded bars represent average percent volume; unshaded bars represent frequency of occurrence.

introduction is intended. Clearly, the evaluation of interspecific impacts which may result from alewife establishment should not be confined to review of limnetic interactions.

Literature Cited

Boaze, J. L. 1972. Effects of landlocked alewife introductions on white bass and walleye populations, Claytor Lake, Virginia. M.S. Thesis, Va. Polytech. Inst. and State Univ., Blacksburg. 103pp.

———, and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150:28–35.

Crowder, L. B. 1980. Alewife, rainbow smelt, and native fishes in Lake Michigan: competition or predation. Environ. Biol. Fishes 5:225–233.

Edsall, T. A. 1964. Feeding by three species of fishes on the eggs of spawning alewives. Copeia 1964:226–227.

Eggers, D. M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Canada 34:290–294.

Fairchild, G. W. 1981. Movement and microdistribution of *Sida crystallina* and other littoral microcrustaceans. Ecology 62:1341–1352.

Gannon, J. E. 1976. The effects of differential digestion rates of zooplankton by alewife, *Alosa pseudoharengus,* on determinations of selective feeding. Trans. Am. Fish. Soc. 105:89–95.

Hall, D. J., E. E. Werner, J. F. Gilliam, G. G. Mittelbach, D. Howard, C. G. Doner, J. A. Dickerman, and A. J. Stewart. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). J. Fish. Res. Board Canada 36:1029–1039.

Hutchinson, B. P. 1971. The effect of fish predation on the zooplankton of ten Adirondak lakes, with particular reference to the alewife, *Alosa pseudoharengus.* Trans. Am. Fish. Soc. 100:325–335.

Janssen, J. 1978. Feeding behavior repertoire of the alewife, *Alosa pseudoharengus,* and the ciscoes, *Coregonis hoyi* and *C. artedii.* J. Fish. Res. Board Canada 35:249–253.

———, and S. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Canadian J. Fish. and Aquatic Sci. 37:177–184.

Kohler, C. C. 1980. Trophic ecology of an introduced, landlocked alewife (*Alosa pseudoharengus*) population and assessment of alewife impact on resident sportfish and crustacean zooplankton communities in Claytor Lake, Virginia. Ph.D. Diss., Va. Polytech. Inst. and State Univ., Blacksburg. 192pp.

———, and J. J. Ney. 1980. Piscivority in a landlocked alewife (*Alosa pseudoharengus*) population. Canadian J. Fish. and Aquatic Sci. 37:1314–1317.

———, and ———. 1981a. Suitability of alewife as a pelagic forage fish for southeastern reservoirs. Proc. Annu. Conf. Southeast. Assoc. Fish & Wildl. Agencies 34:272–286.

———, and ———. 1981b. Consequences of an alewife die-off to fish and zooplankton in a mainstream reservoir. Trans. Am. Fish. Soc. 110:360–369.

Kutkuhn, J. H. 1958. Notes on the precision of numerical and volumetric plankton estimates from small-sample concentrates. Limnol. and Oceanography 3:69–83.

Lagler, K. F. 1956. Freshwater Fishery Biology. W. C. Brown, Dubuque, Iowa. 421pp.

McComish, T. S. 1967. Food habits of bigmouth and smallmouth buffalo in Lewis and Clark Lake and the Missouri River. Trans. Am. Fish. Soc. 96:70–74.

Ney, J. J. 1981. Evolution of forage-fish management in lakes and reservoirs. Trans. Am. Fish. Soc. 110:725–728.

———, C. C. Kohler, and A. A. Nigro. 1982. Landlocked alewife in Claytor Lake, Virginia: evaluation as a forage species for inland waters. Management Publication Number 4, Department of Fisheries and Wildlife Sciences, Va. Polytech. Inst. and State Univ., Blacksburg. 72pp.

Nigro, A. A., and J. J. Ney. 1982. Reproduction and early life accomodations of landlocked alewives to a southern range extension. Trans. Am. Fish. Soc. 111:559–569.

Redfield, G. W., and C. R. Goldman. 1980. Diel vertical migration by males, females, copepodids, and nauplii in a limnetic population of *Diaptomus*. Hydrobiologia 74:241–248.

Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 99:754–765.

Warshaw, S. J. 1972. Effects of alewives (*Alosa pseudoharengus*) on zooplankton of Lake Mononskopomuc, Connecticut. Limnol. and Oceanography 17:816–825.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. and Oceanography 15:556–565.

———, and A. L. McLain. 1972. Lake Michigan: effects of exploitation, introduction, and eutrophication on the salmonid community. J. Fish. Res. Board Canada 29:889–898.

Whiteside, M. C., and J. B. Williams. 1976. A new sampling technique for aquatic ecologists. Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie 19:1534–1539.

Windell, J. T., and S. H. Bowen. 1978. Methods for study of fish diets based on analysis of stomach contents. Pages 219–226 *in* T. Bagenal, ed. Methods for assessment of fish production in freshwater. 3rd ed., Blackwell Scientific Publ., London.