Journal of Fish Biology (1997) **50,** 870–877

An experimental study on the natural removal of dead trout fry in a Lake District stream

J. M. ELLIOTT

NERC Institute of Freshwater Ecology, The Windermere Laboratory, Far Sawrey, Ambleside, Cumbria LA22 0LP, U.K.

(*Received 19 October 1996; Accepted 9 November 1996*)

The chief objective was to discover why few moribund or dead *Salmo trutta* fry were observed on the stream bed when mortality within the stream was known to be high (*c.* 13 000 dead fry year^{-1} for whole stream). Newly dead fry were placed in 20 boxes embedded in the stream bed (20 fry of known total weight per box) and arranged in pairs with one box open and one closed. One pair was removed every 2 days, the fish remains being weighed and the invertebrates in the open box being identified and counted. The experiments were performed from late April to early May in 1967, 1968, 1969 and the results were similar in each year. Both wet and dry weights of fry decreased exponentially but the rate of decrease was much higher in the open boxes; detectable fish remains were about 55% of initial weights after 20 days (end of experiment) in closed boxes but zero after 16 days in open boxes. Invertebrate scavengers were responsible for the higher loss rates in the open boxes and showed a definite succession with caddis larvae and carnivorous stonefly larvae dominant at first, but then being replaced by detritivorous stonefly larvae and freshwater shrimps. These experiments show clearly why dead fry disappear rapidly from the stream bed.

Key words: *Salmo trutta*; fry removal; invertebrate scavengers; Black Brows Beck.

INTRODUCTION

It is now well established that Pacific salmon, *Oncorhynchus* spp., in western North America usually die after spawning and that their decomposing bodies provide an important source of nutrients for the trophic system of their spawning rivers and streams (references in Bilby *et al.*, 1996). Salmon-derived organic matter is incorporated into the stream biota through direct consumption by benthic invertebrates, and by sorption onto the stream-bed substratum of dissolved organic matter released by the decomposing carcasses. Larvae of stoneflies (Plecoptera) and caddisflies (Trichoptera) appear to be the chief scavengers but opinions differ as to their importance. For example, Kline *et al.* (1994) observed these invertebrates feeding on the carcasses whereas Schuldt & Hershey (1995) reported very little use of carcasses by invertebrates. Caddis larvae were also seen feeding on carcasses of squawfish *Ptychocheilus oregonensis* (Richardson) that were eradicated deliberately by poison in a North American river (Brusven & Scoggan, 1969).

Quantitative experimental work on decomposition processes in freshwater fish is restricted to three studies, all in North America: carcasses of bluegills *Lepomis macrochirus* (Rafinesque) with a wet weight range of 12–20 g in Lake Wingra, Wisconsin (Kitchell *et al.*, 1975), and carcasses of rainbow trout, *Oncorhynchus*

Tel.: +44 (0) 15394 42468/9; fax: +44 (0) 15394 46914.

0022–1112/97/040870+08 $25.00/0/jb960355

mykiss (Walbaum), with a wet weight range of 84–156 g in a freshwater marsh in Wyoming (Parmenter & Lamarra, 1991) and with mean wet weights of 103 g in spring and 146 g in summer in Mink Creek, Idaho (Minshall *et al.*, 1991). Carcass loss rates were higher in summer than winter, e.g. decay completed in about 50 days in summer but >120 days in winter in Mink Creek. Fish mass generally decreased in these studies according to an exponential model. There is no similar information on the decomposition of small fish, including juvenile salmonids. Invertebrate predators attack the eggs and early life stages of freshwater fish, including salmonids (McDonald, 1960; McNeil *et al.*, 1964; Newberg, 1974; Fox, 1978; Brown & Diamond, 1984; Diamond, 1986; Diamond & Wakefield, 1986; Rubin & Svensson, 1993). There is therefore a high probability that invertebrates facilitate the removal of dead and moribund salmonids in the early stages of the life cycle, but no studies have confirmed this.

The present investigation originates from an assessment of loss rates in the juvenile stages of a sea trout *Salmo trutta* L., population in Black Brows Beck (Elliott, 1986, 1994). Losses from the population were due to mortality within the stream and fish moving downstream to leave the stream. Catches in a trap at the stream mouth and estimates of population density within the stream showed that losses due to emigration contributed 22% to the estimated total losses of fry in the critical period for survival in the early stages of the life cycle. Therefore, population losses of fry were due chiefly to mortality within the stream rather than to migration. Although such losses are considerable (e.g. *c.* 13 000 fry for the whole stream with a total area of 420 m^2; see Elliott, 1986), few moribund or dead fry were ever observed on the stream bed. The purpose of the present experimental investigation was to explain this apparent paradox.

MATERIALS AND METHODS

Experiments were performed on fry (the short transition stage when the trout emerge from the gravel and start to feed on invertebrates) from Black Brows Beck, a small nursery stream for sea trout in NW England at the southern edge of the Lake District. The stream and the results of the long-term study on the trout population are described in detail in Elliott (1994). Downstream-moving fry were caught in nets and a trap at the stream mouth from late April to early May in 1967, 1968 and 1969. Most of the fry were dead or moribund, were underweight for their length, and had a higher water content and lower fat and energy contents compared with fry in good condition (Elliott, 1986, 1993). These are all typical signs of starvation, which was probably the chief cause of death although it is not known if other factors, such as parasites and disease, were involved.

Newly collected dead and moribund fry were kept in a covered tank in the stream and the interval between capture and the start of an experiment never exceeded 2 h. Moribund fry were allowed to die naturally in the tank, and were not used in the experiments if still alive. A batch of 20 dead fry was weighed (wet weight to nearest mg) and placed in a wooden box (inside dimensions 25 × 25 cm with height of 8 cm). Dry weights were determined for 13 batches of 20 fry after drying at 105° C in a hot-air oven until a constant weight was obtained (see methods in Elliott, 1976). Dry weight was directly proportional to wet weight, the mean water content being 87·5% (95% CL ± 0·766, n=13). Therefore, dry weights were assumed to be 12·5% of wet weights for the initial dry weights of the 20 fry in each box. The bottom of the box was a coarse mesh covered with fine mesh nylon netting (mesh 390 μm) to prevent the entry of benthic invertebrates. The sliding top of the box was covered with the same netting. Before adding the fry, the interior bottom of the box was covered with small stones (diameter

2–4·5 cm) and some decaying leaf material from the stream bed. Care was taken that no invertebrate animals were introduced with the material and some field trials with closed boxes devoid of fry confirmed the absence of invertebrates. The box was then embedded in the stream bed.

There were 10 closed boxes and 10 open boxes with their lids replaced with wide mesh (mesh width 5 mm) to allow the entry of invertebrates but not fish. The boxes were arranged in pairs (one closed, one open) down the length of the stream with 20 fry in each box. One pair of boxes was selected at random after 2 days in the stream and their contents removed; the fish remains were weighed (both wet and dry weights with the latter determined directly from the fish remains, method as above) and the invertebrates identified and counted. This process was repeated every 2 days so that the last pair of boxes was removed 20 days after the start of the experiment. The experiments were performed from late April to early May in 1967, 1968 and 1969. Water temperatures during each 20-day experiment were similar in 1967 and 1969, but slightly higher in 1968, with mean values and ranges of 7·2° C (4·0–10·9° C) for 1967, 8·1° C (4·1–12·9° C) for 1968 and 7·2° C (4·3–10·0° C) for 1969.

Mean values for the initial wet weights of 20 fry in each box were not significantly different ($P>0{\cdot}05$) for open and closed boxes in the three years, geometric means (with 95% CL) for 1967, 1968, 1969 respectively being 2380 mg (2270–2496 mg), 2437 mg (2333–2546 mg), 2395 mg (2281–2514 mg) for open boxes, and 2420 mg (2329–2514 mg), 2396 mg (2307–2489 mg), 2425 mg (2324–2531 mg) for closed boxes. However, the initial wet weights varied considerably between the 10 boxes in each experiment with ranges of 2176–2591 mg for open boxes and 2186–2592 mg for closed boxes. Therefore, weights of fish remains in each box were expressed as a percentage of the initial weight of 20 fry in the same box.

As mentioned in the introduction, previous studies have shown that the weight of the decaying fish decreases usually according to an exponential model and this was also appropriate in the present study. The relationship between the weight of fish remains expressed as a percentage of the weight of 20 fry at the start of the experiment (W%) and the time from the start of the experiment (t days) was given by:

$$W = a\mathrm{e}^{-bt} \tag{1a}$$

or in linear form:

$$\ln W = \ln a - bt \tag{1b}$$

where a and b are constants estimated by linear regression.

RESULTS

Assuming a 100% initial weight on day 0, there were potentially 11 values in each data set for open and closed boxes (Fig. 1). However, this number was appropriate for only the dry weights in closed boxes ($n=11$ for each year in Table I). Wet weights increased in the first 2 days of the experiments in both closed and open boxes because water entered the dead fish [Fig. 1(a)], and therefore only values from day 2 onwards were included in the analyses ($n=10$ for wet weight in closed boxes). No fish remains were found in the open boxes after day 16 and therefore there were only eight and nine values in each year for wet and dry weights respectively [Fig. 1(a) and (b); Table I]. The exponential model [equation (1a)] was an excellent fit to the data sets ($P<0{\cdot}01$ for all regression equations in Table I). Values of the constants $\ln a$ and b in equation (1b) varied between the data sets for the 3 years but none of the differences was significant ($P>0{\cdot}05$). Therefore, regression equations were calculated for the combined data

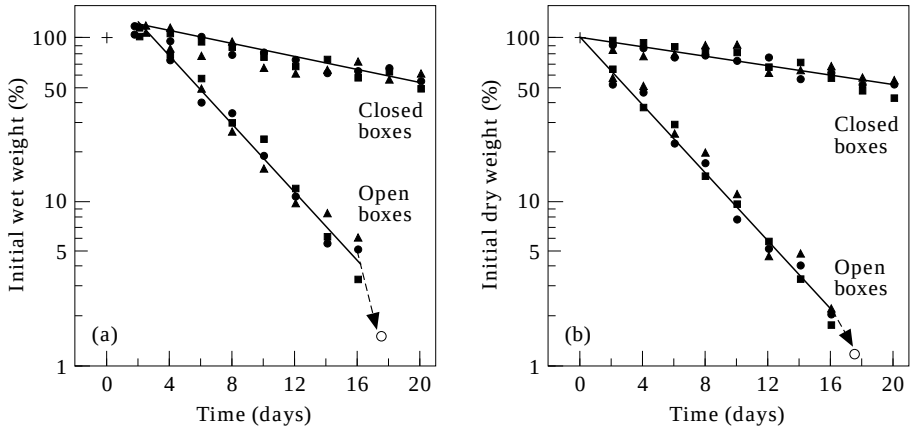

FIG. 1. Relationship between either (a) wet weight or (b) dry weight of fish remains expressed as a percentage of the initial weight of 20 dead fry at the start of the experiment (W% on log scale) and time (t days) from the start of the experiment for closed and open boxes. Symbols are for experiments in different years: ●, 1967; ■, 1968; ▲, 1969; regression lines are given by equation (1b) with parameter estimates for all years combined (Table I).

sets for the 3 years (all years in Table I) and these were used to fit the regression lines in Fig. 1(a) and (b). Coefficients of determination were all high (r^2>0·77 in Table I), indicating that most of the variation in wet or dry weights could be explained by exponential decrease in weight with time.

There were clear differences between the open and closed boxes. The weight of fish remains decreased slowly to 55% of the initial wet weights and 54% of the initial dry weights after 20 days in the closed boxes, but decreased rapidly to zero after 16 days in the open boxes [Fig. 1(a) and (b)]. Invertebrate scavengers were responsible for the rapid decrease in the open boxes. None was found in the closed boxes and fish decay appeared to be due to micro-organisms, the fish being covered with fungi after day 6.

Invertebrate colonization was rapid in the open boxes and the succession of the major groups was illustrated by comparing the exponential decrease in fish remains with the number of invertebrates found in the boxes on successive days [Fig. 2(a) and (b)]. The pattern of succession was similar in the 3 years. Caddis larvae and carnivorous stonefly larvae were dominant at first and consumed large pieces torn from the dead fry, thus speeding up the disintegration of the corpse. Of the 117 caddis larvae found in the boxes over the 3 years, most (86) were *Odontocerum albicorne* (Scopoli), with 22 *Rhyacophila dorsalis* (Curtis), eight *Potamophylax cingulatus* (Stephens) and one *Halesus radiatus* (Schrank). Of the 38 carnivorous stoneflies found in the 3 years, most (23) were *Chloroperla tripunctata* (Scopoli), with seven *Perla bipunctata* Pictet, six *Siphonoperla torrentium* (Pictet) and two *Isoperla grammatica* (Poda). After day 6, these two groups were replaced, almost completely by day 10, by freshwater shrimps, *Gammarus pulex* L., and detritivorous stonefly larvae [totals for 3 years: 105 *Amphinemura sulcicollis* (Stephens), 59 *Leuctra inermis* Kempny, 11 *Nemoura* spp., nine *L. fusca* (L.)]. These two groups removed the remaining bits of fry rapidly so that no detectable remains could be found after day 16. Mayfly (Ephemeroptera) larvae also colonized the boxes but appeared to be feeding on

TABLE I. Values of ln a (± 95% CL) and b (± 95% CL) in equation (1b), with number (n) of values used in the regression, and coefficients of determination (r^2) adjusted for small samples

	ln a ± 95% CL	b ± 95% CL	n	r^2
Wet weight				
Closed boxes				
1967	4·771 ± 0·109	− 0·036 ± 0·009	10	0·907
1968	4·819 ± 0·089	− 0·042 ± 0·007	10	0·952
1969	4·810 ± 0·202	− 0·040 ± 0·016	10	0·774
All years	4·800 ± 0·069	− 0·039 ± 0·006	30	0·878
Open boxes				
1967	5·215 ± 0·265	− 0·231 ± 0·026	8	0·985
1968	5·435 ± 0·339	− 0·252 ± 0·034	8	0·979
1969	5·178 ± 0·287	− 0·221 ± 0·028	8	0·981
All years	5·276 ± 0·146	− 0·234 ± 0·014	24	0·980
Dry weight				
Closed boxes				
1967	4·599 ± 0·088	− 0·030 ± 0·007	11	0·893
1968	4·688 ± 0·102	− 0·039 ± 0·009	11	0·911
1969	4·608 ± 0·113	− 0·027 ± 0·010	11	0·802
All years	4·632 ± 0·055	− 0·032 ± 0·005	33	0·860
Open boxes				
1967	4·606 ± 0·223	− 0·237 ± 0·023	9	0·986
1968	4·688 ± 0·153	− 0·247 ± 0·016	9	0·994
1969	4·672 ± 0·275	− 0·233 ± 0·029	9	0·978
All years	4·655 ± 0·111	− 0·239 ± 0·012	27	0·985

the epilithon on the stones and box sides, rather than on the fish remains (totals for 3 years: 226 *Baetis rhodani* (Pictet), 21 *B. muticus* (Burmeister), four *Rhithrogena semicolorata* (Curtis).

DISCUSSION

This experimental study shows clearly why dead trout fry disappear rapidly from the stream bed and therefore why few moribund or dead fry are ever observed in streams such as Black Brows Beck. There are only two other experimental studies on decomposition rates in salmonids. Although they are on much larger fish, some comparisons of loss rates are possible. In studying decomposition rates of large rainbow trout in a freshwater marsh, Parmenter & Lamarra (1991) deliberately chose a site lacking shrimps and crayfish because they considered that these scavengers would speed up the decay process. Loss rates for the rainbow trout, in terms of dry weight, were almost 6% day^{-1} at water temperatures often exceeding 10° C. In the second study, also on large rainbow trout, Minshall *et al.* (1991) obtained loss rates, in terms of dry weight, of 1·54% day^{-1} in winter–spring experiments and 4·68% day^{-1} in summer at temperatures in the range 0·5–11° C and 6·5–10·8° C respectively. Loss rates

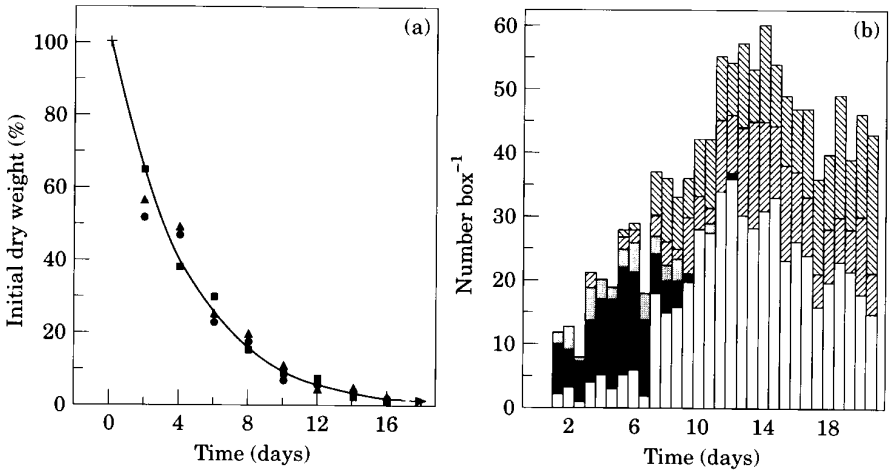

FIG. 2. (a) Relationship between dry weight of fish remains expressed as a percentage of the initial weight of 20 dead fry at the start of the experiment (W% on arithmetic scale) and time (t days) from the start of the experiment for open boxes (symbols and regression line as in Fig. 1). (b) Changes in the numbers of invertebrates colonizing the open boxes from the start of the experiment. Note that for each sampling day there are three columns corresponding to the experiments in 1967, 1968 and 1969. ▧, Mayflies; ▨, stoneflies (detritivorous); ▩, stoneflies (carnivorous); ■, caddis; □, shrimp.

were obtained also from the exponential rates in the present study, using the values of b in Table I (% loss rate day$^{-1} = 1 - e^{-b}$). Values in terms of dry weight varied between years in the range 2·66–3·82% day^{-1} for closed boxes at mean temperatures in the range 7–8° C. In spite of the different temperatures and fish sizes in the three studies, these values are within the range obtained by Minshall *et al.* (1991) and only slightly less than the value obtained at higher temperatures by Parmenter & Lamarra (1991).

As noted above, invertebrates were not a major factor in the two previous studies and this is probably why loss rates were similar to those obtained in the closed boxes of the present study. Loss rates in the absence of invertebrates therefore vary in the range 1·5–6·0% day^{-1} depending on water temperature. These values are clearly well below those obtained in the open boxes; loss rates for the combined data for all years being 20·86% day^{-1} (range for different years: 19·83–22·28) for wet weight and 21·26% day^{-1} (range: 20·78–21·89) for dry weight. Clearly, invertebrates speed up the process for the removal of dead fish.

There was a definite succession of different invertebrate groups during the removal process. Caddis larvae were the first group to demolish the dead fry. The same four species recorded in the present study were identified also as the chief predators of eggs of the bullhead *Cottus gobio* L., from a southern chalk stream whilst other potential predators, including two caddis species, did not eat the eggs (Fox, 1978). *Odontocerum albicorne* was the chief scavenger amongst the caddis species found in the open boxes. This omnivorous species is most active at night but attacks live invertebrates rarely, whereas it eats dead and moribund invertebrates readily (Elliott, 1970). It takes 1 year to complete its life cycle in Black Brows Beck and the major growth period for the older larvae is in spring (Elliott, 1982) when dead trout fry are readily available as food. As the

larvae can travel up to 10 m in a night whilst searching for food, it is not surprising that they were soon found in the open boxes in the present study. Caddis larvae also consume the eggs of perch *Perca fluviatilis* L., but invertebrates in general do not appear to be important predators of perch eggs (Diamond & Wakefield, 1986). In contrast, serological studies have shown invertebrates to be important as scavengers of rainbow trout eggs (Brown & Diamond, 1984), and as predators of eggs and juveniles of roach *Rutilus rutilus* (L.) (Diamond, 1986).

Most benthic invertebrates in streams are active at night and will soon locate potential food. They do, however, have different particle-size preferences and these are reflected in the succession shown in the open boxes [Fig. 2(b)]. Once the dead fry had been disintegrated by the caddis larvae and carnivorous stonefly larvae in the first 6 days of each experiment, shrimps and detritivorous stonefly larvae consumed the remaining smaller pieces so that no fish remains were found after day 16. However, reduced numbers of these scavengers were still present in the open boxes until the end of the experiment, suggesting that very small pieces of fish were still available as food. The overall benefit to the stream ecosystem is that a large amount of trout production in the early life stages is recycled within the stream rather than being exported and lost.

References

Bilby, R. E., Fransen, B. R. & Bisson, P. A. (1996). Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 164–173.

Brown, A. F. & Diamond, M. (1984). The consumption of rainbow trout (*Salmo gairdneri* Richardson) eggs by macroinvertebrates in the field. *Freshwater Biology* **14,** 211–215.

Brusven, M. A. & Scoggan, A. C. (1969). Sarcophagous habits of Trichoptera larvae on dead fish. *Entomological News* **80,** 103–105.

Diamond, M. (1986). Some studies of predation by invertebrates on the eggs and young of freshwater fish: a race against time. *Proceedings of the Fourth British Freshwater Fish Conference* (O'Hara, K., Aprahamian, C. & Leah, R. T., eds), pp. 135–144. Liverpool: University of Liverpool Press.

Diamond, M. & Wakefield, P. M. (1986). The consumption of eggs of the perch, *Perca fluviatilis* L., by macroinvertebrates in the field. *Freshwater Biology* **16,** 373–376.

Elliott, J. M. (1970). The diel activity patterns of caddis larvae (Trichoptera). *Journal of Zoology* **160,** 279–290.

Elliott, J. M. (1976). Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. *Journal of Animal Ecology* **45,** 273–289.

Elliott, J. M. (1982). A quantitative study of the life cycle of the case-building caddis *Odontocerum albicorne* (Trichoptera: Odontoceridae) in a Lake District stream. *Freshwater Biology* **12,** 241–255.

Elliott, J. M. (1986). Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. *Journal of Animal Ecology* **55,** 907–922.

Elliott, J. M. (1993). The pattern of natural mortality throughout the life cycle in contrasting populations of brown trout, *Salmo trutta* L. *Fisheries Research* **17,** 123–136.

Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout.* Oxford University Press, Oxford.

Fox, P. J. (1978). Caddis larvae (Trichoptera) as predators of fish eggs. *Freshwater Biology* **8,** 343–345.

Kitchell, J. F., Koonce, J. F. & Tennis, P. S. (1975). Phosphorus flux through fishes. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **19,** 2478–2484.

Kline, T. C., Goering, J. J., Mathisen, O. A., Poe, P. H., Parker P. L. & Scalan, R. S. (1994). Recycling of elements transported upstream by runs of Pacific salmon: I. δ^{15}N and δ^{13}C evidence in Kvichak River watershed, Bristol Bay, southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 2350–2365.

McDonald, J. G. (1960). A possible source of error in assessing the survival of Pacific salmon eggs by redd sampling. *The Canadian Fish Culturist* **26,** 27–30.

McNeil, W. J., Wells, R. A. & Brickell, D. C. (1964). Disappearance of dead pink salmon eggs and larvae from Sashin Creek, Baranof Island, Alaska. *Special Scientific Report of the U.S. Fish and Wildlife Service* **485,** 1–13.

Minshall, G. W., Hitchcock, E. & Barnes, J. R. (1991). Decomposition of rainbow trout (*Oncorhynchus mykiss*) carcasses in a forest stream ecosystem inhabited only by nonanadromous fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* **48,** 191–195.

Newberg, H. J. (1974). Planarians as a mortality factor on spawned fish eggs. *Progressive Fish Culturist* **36,** 227–230.

Parmenter, R. R. & Lamarra, V. A. (1991). Nutrient cycling in a freshwater marsh: the decomposition of fish and waterfowl carrion. *Limnology and Oceanography* **36,** 976–987.

Rubin, J.-F. & Svensson, M. (1993). Predation by the noble crayfish, *Astacus astacus* (L.), on emerging fry of sea trout, *Salmo trutta* (L.). *Nordic Journal of Freshwater Research* **68,** 100–104.

Schuldt, J. A. & Hershey, A. E. (1995). Effect of salmon carcass decomposition on Lake Superior tributary streams. *Journal of the North American Benthological Society* **14,** 259–268.