The above data clearly demonstrate selectivity in the diets of the four common species that show predation on other coelenterates. However, no predator was dependent on a single prey species. It is difficult to evaluate the degree of competition involved. Not only do the four species vary in period of maximum abundance in the bay but all four species will accept noncoelenterate prey. This study will be extended to investigate predation on other possible prey including fish larvae.

Acknowledgments — We are very grateful for the facilities of the Pacific Biological Station, Nanaimo, B.C., where this study was carried out and the cooperation of the staff. Dr Z. Kabata kindly translated several Russian papers. Miss Valerie Overend assisted in collection of specimens. The project was supported by NRC Grant A2007 to M.N.A.

AGASSIZ, L. 1862. Contribution to the natural history of the United States of America. Second Monograph. IV. Hydroidae 4: 183–372. pl. 16–35.

FORBES, E. 1848. A monograph of the British naked eyed medusae with figures of all the species. The Ray Society Publication, London. 104 p., pl. 1–13.

FRASER, J. H. 1969. Experimental feeding of some medusae and Chaetognatha. J. Fish. Res. Board Can. 26: 1743–1762.

GREVE, W. 1970. Cultivation experiments on North Sea ctenophores. Helgol. Wiss. Meeresunters. 20: 304–317.

1971. Okologische Untersuchungen an *Pleurobrachia pileus*. 1. Freilanduntersuchungen. Helgol. Wiss. Meeresunters 22: 303–325.

1972. Okologische Untersuchungen an *Pleurobrachia pileus*. 2. Laboratoriumsuntersuchungen. Helgol. Wiss. Meeresunters. 23: 141–164.

HUNTLEY, M. C., AND L. A. HOBSON. 1978. Medusa predation and plankton dynamics in a temperate fjord, British Columbia. J. Fish. Res. Board Can. 35: 257–261.

HUSING, J. O. 1956. Zur Frage der Ernahrung der Ohrenqualle *Aurelia aurita* L. (Scyphozoa, Semaeostomae). Wiss. Martin Luther Univ. Halle-Wittenberg Math. Naturwiss Reihe 5(3): 479–482.

HYMAN, L. H. 1940. Observations and experiments on the physiology of medusae. Biol. Bull. (Woods Hole) 79: 282–296.

LEBOUR, M. V. 1922. The food of plankton organisms. J. Mar Biol. Assoc. U.K. 12: 644–677.

1923. The food of plankton organisms II. J. Mar. Biol. Assoc. U.K. 13: 70–92.

LOGINOVA, N. P., AND N. M. PERZOVA. 1967. Some data on ecology of feeding of pelagic Coelenterata in the White Sea. Issled. Fauny Morei 7(15): 21–28. (In Russian)

MCCORMICK, J. M. 1969. Trophic relationships of hydromedusae in Yaquina Bay, Oregon. Northwest Sci. 43: 207–214.

PETIPA, T. S., E. V. PAVLOVA, AND G. N. MIRONOV. 1970. The food web structure utilization and transport of energy by trophic levels in the planktonic communities, p. 142–167. *In* J. H. Steele [ed.] Marine food chains. Oliver and Boyd, Edinburgh. 552 p.

PLOTNIKOVA, E. D. 1961. On the diet of medusae in the littoral of Eastern Murman, p. 153–156. *In* M. M. Kamshilov [ed.] Hydrological and biological features of the shore waters of Murman. Akad. Nauk USSR Kolsk. Fil. (In Russian)

SOUTHWARD, A. J. 1955. Observations on the ciliary currents of the jelly-fish *Aurelia aurita* L. J. Mar. Biol. Assoc. U.K. 34: 201–216.

SVESHNIKOV, V. A. 1963. The feeding habits of jelly-fish as possible rivals of the White Sea herring. Moscow Univ. Belmorsk. Biologichesk. Tr. 2: 246–249. (In Russian; English abstract)

ZELICKMAN, E. A. 1976. The biology of a little known neritic hydromedusa *Polyorchis karafutoensis* (Polyorchidae: Coelenterata). Tr. Inst. Okeanol. Akad. Nauk SSSR. 105: 210–213. (In Russian; English abstract)

ZELICKMAN, E. A., V. I. GELFAND, AND M. A. SHIFRIN. 1969. Growth, reproduction and nutrition of some Barents Sea hydromedusae in natural aggregations. Mar. Biol. (Berl.) 4: 167–173.

Leaf Litter Processing in a Regulated Rocky Mountain Stream

ROBERT A. SHORT[1] AND JAMES V. WARD

Department of Zoology and Entomology, Colorado State University, Fort Collins, CO 80523, USA

SHORT, R. A., AND J. V. WARD. 1980. Leaf litter processing in a regulated Rocky Mountain stream. Can. J. Fish. Aquat. Sci. 37:123–127.

Processing of alder (*Alnus tenuifolia*) was investigated during autumn and winter to determine the influence of stream regulation on leaf litter processing. Study sites were the Colorado River below Granby Dam and the Fraser River, an unregulated tributary. Alder leaves (5-g units) were attached to bricks and placed in riffles. Leaching controls were retrieved after 48 h; thereafter five replicates were collected from each site after 17, 38, 52, and 66 d. There were significant differences ($P < 0.05$) in processing rates between sites. The loss rate coefficient (k) was much higher ($k = 0.0462$) for leaves incubated in the regulated section

---

[1] Present address: Department of Biological Sciences, North Texas State University, Denton, TX 76203, USA.

Printed in Canada (J5676)
Imprimé au Canada (J5676)

of the Colorado River than for those in the unregulated tributary ($k = 0.0235$). The hypothesis that reductions in macroinvertebrate shredders would decrease processing rates of leaf litter in regulated streams was not supported by the results. The "winter warm" thermal regime below the reservoir seems to compensate for the virtual absence of shredder species apparently by enhanced microbial processing.

Key words: Colorado River, leaf litter, macroinvertebrates, Rocky Mountains, stream regulation, temperature

SHORT, R. A., AND J. V. WARD. 1980. Leaf litter processing in a regulated Rocky Mountain stream. Can. J. Fish. Aquat. Sci. 37: 123–127

Dans le but de déterminer l'influence du contrôle d'un cours d'eau sur la transformation de la litière de feuilles dans un cours d'eau des montagnes Rocheuses, nous avons étudié la transformation de l'aulne (*Alnus tenuifolia*) en automne et en hiver. Les recherches ont été effectuées sur le fleuve Colorado, en aval du barrage Granby et sur la rivière Fraser, un tributaire non contrôlé. Des feuilles d'aulne (unités de 5 g) furent attachées à des briques et placées dans des «maigres» le 29 septembre. Des témoins de lessivage furent enlevés après 48 h; par la suite, 5 reproductions furent recueillies à chaque site après 17, 38, 52 et 66 jours. Il y a des différences significatives ($P < 0{,}05$) de taux de transformation entre les sites. Le coefficient de taux de perte (k) est beaucoup plus élevé ($k = 0{,}0462$) pour des feuilles incubées dans la section contrôlée du fleuve Colorado que celles placées dans le tributaire non contrôlé ($k = 0{,}0235$). Les résultats de cette étude n'appuient donc pas l'hypothèse que la diminution des macroinvertébrés déchiqueteurs ralentit la transformation de la litière végétale dans des cours d'eau contrôlés. Le régime thermique de «chaleur hivernale» en aval du réservoir semble compenser l'absence virtuelle d'espèces déchiqueteuses par une transformation microbienne plus active.

Received June 15, 1979
Accepted October 4, 1979

Reçu le 15 juin 1979
Accepté le 4 octobre 1979

DETERMINATIONS of leaf litter processing rates have generated a great deal of information concerning stream ecosystem structure and function (e.g. Petersen and Cummins 1974; Sedell et al. 1975; Benfield et al. 1977) and have provided an experimental means to test various hypotheses (Reice 1974, 1977). The leaf pack method has also been used as a bioassay to determine the effects of man's activities on streams (Triska and Sedell 1976; Gelroth and Marzolf 1978). One significant anthropogenic impact has been the construction of numerous reservoirs on previously free-flowing streams. Large dams may greatly modify the physicochemical conditions of downstream reaches with resultant changes in the diversity, density, and composition of the macroinvertebrate fauna (Ward 1976a; Ward and Stanford 1979). Since there is a selective elimination of certain taxonomic and functional groups (Ward and Short 1978), it was hypothesized that leaf litter processing would be altered by stream regulation. The leaf pack method was utilized to determine the influence of stream regulation by dams on leaf litter processing rate.

Materials and methods — Study area — Study sites were on the Colorado River below Lake Granby and on the Fraser River, a major tributary unregulated by dams. Lake Granby is a large storage reservoir located 10 km northeast of Granby in the Rocky Mountains of northern Colorado. The dam is 91 m high and impounds 666×10^6 m^3 of water. The confluence of the Fraser and Colorado rivers is 12 km below Granby Dam. A site on the Fraser River was selected immediately upstream from Granby.

Study locations were at comparable elevations (2460 and 2420 m a.s.l.) and exhibited generally similar conditions. Woody riparian vegetation consisted predominantly of willows (*Salix* spp.) and alder (*Alnus tenuifolia*) and the stream bottom was predominantly rubble in both study sections. During the study period, discharge averaged 0.54 m^3/s in the Colorado River and 0.53 m^3/s in the Fraser River. Total dissolved solids (35.7 mg/L; 65.4 mg/L) and methyl orange alkalinity (11.0 mg/L; 22.5 mg/L) values were somewhat higher in the Fraser River. Nitrogen–nitrate (53 μg/L; 43 μg/L) and pH (7.6; 7.4) exhibited similar values at both locations. There were, however, considerable differencs in water temperature (discussed later) between the regulated and unregulated streams.

Experimental procedures — Alder (*Alnus tenuifolia*) leaves were collected in September 1978 immediately prior to abscission. The leaves were air-dried then oven-dried at 60°C for 48 h and weighed into 5-g units and strung on monofilament line. A single leaf pack was lashed to each brick and placed into a riffle area of each stream on September 29. After 48 h, three replicate leaf packs were retrieved from each site to serve as leaching controls. Thereafter five replicates were collected from each site after 17, 38, 52, and 66 d in the stream. At the time of collection the leaf pack was cut free of the brick and placed into a plastic bag containing 5% formalin. In the laboratory the leaf pack was thoroughly rinsed with tap water to remove accumulated sediments, dried at 60°C for 48 h, and weighed (± 0.1 g). Macroinvertebrates associated with the leaf pack were placed into 80% EtOH until identified and enumerated. Dry weight of macroinvertebrates was determined following drying to constant weight at 60°C. No attempt was made to correct for weight loss during preservation. Water temperatures were monitored using maximum–minimum thermometers at each site.

Results — There were clear difference in leaf processing rates (Fig. 1A). On each sampling date leaf packs from the Colorado River had less weight remaining than those from the Fraser River. Analysis of variance showed these differences to be significant ($P <$

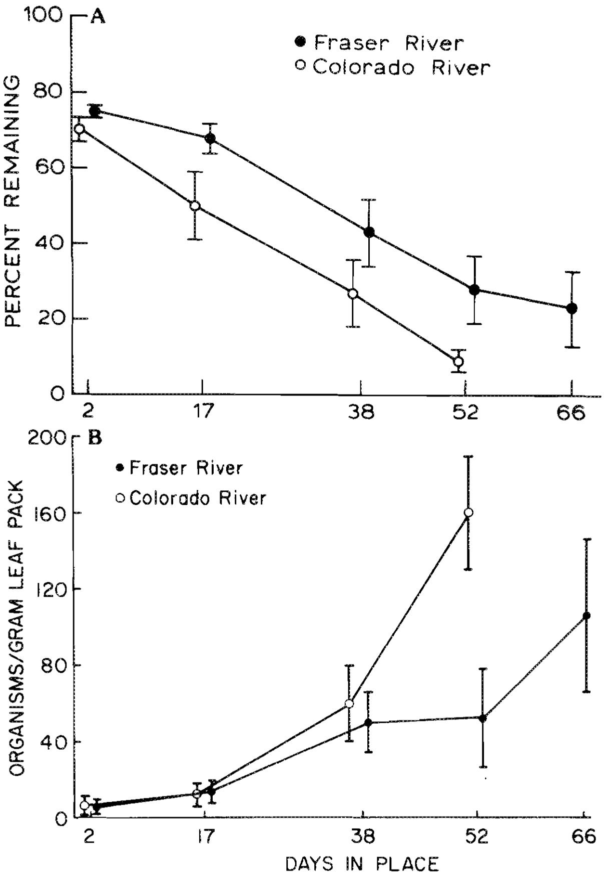

FIG. 1. A) Decomposition of alder leaf packs in the Fraser River and Colorado River, Colorado, September 29 through December 3, 1978. Mean value ± 1 SD; B) Colonization of leaf packs by macroinvertebrates plotted as organisms per dry weight of leaf pack remaining. Mean value ± 1 SD.

0.05) on each sampling date except day 38 ($0.05 < P < 0.10$). Even losses due to leaching exhibited significant differences between sites. Gelroth and Marzolf (1978) found that leaf packs apparently lost weight by leaching to a greater degree in a natural stream than a channelized stream. These results are difficult to reconcile since leaching is thought to be a purely physical process unrelated to variables such as temperature (Petersen and Cummins 1974).

Leaf packs collected from the Colorado River site were >90% processed after 52 d in the stream (Fig. 1A). Thus leaf packs were not again collected at this site. The Fraser River samples collected on January 7 (day 100) consisted only of monofilament line as either the leaf packs had been completely processed or were damaged by ice action. The leaf packs collected on this date were therefore not included in the analysis.

After accounting for leaching losses, linear regression was used to estimate the loss rate coefficient (k) following $\log_e$ transformation of the percent remaining data in Fig. 1A. This assumes that leaf pack processing in streams follows an exponential decay model (Petersen and Cummins 1974). These estimates are presented below along with calculated times for 50 and 90% processing.

Site	k	50%	90%
Colorado River	0.0462	15	50
Fraser River	0.0235	30	98

The k values for both sites indicate rapid processing of alder leaf packs with the Colorado River loss rate coefficient approximately twice that of the Fraser River. Leaves with k values above 0.010 are considered "fast" species (Petersen and Cummins 1974). Alder leaf packs would be 90% processed in just 50 d at the Colorado River site, a rate of processing nearly equal to that obtained by Hart and Howmiller (1975) for *Alnus rhombifolia* leaves in a much warmer southern California stream.

Although numbers of macroinvertebrates per leaf pack were generally similar at the two sites (Fig. 1B), there were obvious differences in the species composition (Table 1). Eight of the taxa collected in the Fraser River leaf packs were not found in the Colorado River samples. Six taxa were collected only from the Colorado River. These differences undoubtedly relate to the effects of stream regulation (Ward and Short 1978). The most abundant species collected at both sites was the mayfly *Ephemerella infrequens* which accounted for 76% of the total number of macroinvertebrates in the Colorado River leaf packs and 34% in the Fraser River samples. Many taxa in the Colorado River leaf packs were present in very low numbers (Table 1); often only 1 or 2 individuals were collected during the entire study period (e.g. *Tricorythodes* sp., *Skwala parallela*, *Pteronarcella badia*, *Lepidostoma* sp.). This occurred to a much lesser degree in the Fraser River leaf packs.

Assignment of the macroinvertebrates to functional groups (Merritt and Cummins 1978) also reveals drastic differences between the sites (Table 2). Collectors were by far the dominant group in the Colorado River leaf packs, mainly due to the presence of large numbers of *Ephemerella infrequens*. Shredders were much less important at the location below Granby Dam. In the Fraser River leaf packs, the collectors formed the bulk of the biomass, but the shredder biomass value was 10× that found in the Colorado River samples. Alder leaves incubated in a small headwater stream in Colorado (Short et al. 1980) had an even greater shredder biomass than the Fraser River samples, yet the loss rate coefficient ($k = 0.0308$) was less than that of the Colorado River below Granby Dam where shredders were virtually absent.

Minimum and maximum water temperatures recorded at intervals over the sampling period are shown below.

Time interval	Colorado River	Fraser River
Oct. 1–Oct. 15	9.4–13.3	1.1–13.1
Oct. 15–Nov. 5	7.2–13.1	0–9.4
Nov. 5–Nov. 19	5.0–10.0	0–5.6
Nov. 19–Dec. 3	4.6–7.8	0
Dec. 3–Jan. 7	1.7–5.3	0

The effect of impoundment was to elevate fall and winter temperatures and to increase thermal constancy (see Ward 1976b).

Discussion — The results of this study do not support our hypothesis that reduction of shredders would result in a slower processing of leaf litter in the regulated stream.

Temperature appears to be one factor to which the differences in leaf processing rates between the streams may be attributed. Weight loss of leaf litter often is directly proportional to stream temperature (Anderson and Sedell 1979). The elevated fall and winter water temperatures resulting from Lake Granby thus appear to provide an explanation for the higher loss rate coefficient in the Colorado River. The "winter warm" thermal regime below the reservoir seems to compensate for the virtual absence of shredder species. Inputs of coarse particulate organic matter (CPOM) are normally reduced below dams (which accounts for reduced shredder populations) since instream transport from upper reaches is eliminated (Ward 1976a). Therefore, CPOM probably plays a minor role in the energetics of regulated stream reaches. Regulated streams are characterized by large standing crops of autotrophs (Ward 1976a) which likely provide the major portion of the food base. What then accounts for the rapid processing of leaf litter below Granby Dam? Enhanced microbial processing at higher temperatures provides at least a partial explanation. It is also possible that surficial scraping by the large numbers of *E. infrequens* significantly contributed to weight loss of Colorado River leaf packs. Elevated temperature may increase leaf weight loss by increasing feeding activities of macroinvertebrates.

TABLE 1. Mean numbers of macroinvertebrates per leaf pack over the entire sampling period. Functional group classification based on Merritt and Cummins (1978): S = shredder, C = collector, G = grazer, and P = predator. + denotes <0.1.

Taxon	Colorado River	Fraser River	Functional group
Ephemeroptera			
Baetis sp.	2.6	6.2	C
Ephemerella grandis	+	1.0	C
Ephemerella infrequens	38.2	26.4	C
Paraleptophlebia sp.	0.5	5.7	C
Rhithrogena sp.	0	1.1	C/G
Tricorythodes sp.	+	0	C
Plecoptera			
Alloperla sp.	0	5.0	P
Skwala parallela	+	0	P
Cultus sp.	0	0.8	P
Claassenia sabulosa	0	+	P
Pteronarcys californica	0	+	S
Pteronarcella badia	0.1	0.1	S
Capnia sp.	0	0.5	S
Trichoptera			
Arctopsyche sp.	0	2.0	C
Hydropsyche sp.	+	2.5	C
Brachycentrus sp.	0.2	0.2	C
Glossosoma sp.	+	0.8	C/G
Lepidostoma sp.	0.1	22.4	S
Rhyacophila angelita	+	0	P
Diptera			
Chironomidae	4.5	2.2	C/G
Simulium sp.	2.1	0.3	C
Atherix pachypus	0.6	0	P
Coleoptera			
Optioservus sp.	0	0.7	C/G
Gastropoda			
Physa sp.	+	0	G
Turbellaria			
Polycelis coronata	1.1	0	P
Total	50.0	77.9	

TABLE 2. Mean biomass of macroinvertebrate functional groups (mg/g leaf pack) collected in leaf packs over the entire sampling period. + denotes <0.1.

Functional group	Colorado River	Fraser River
Collectors	40.9	10.3
Shredders	0.2	2.0
Predators	1.4	2.0
Grazers	+	+
Total	42.5	14.3

It is not known whether the findings of the present study are applicable to regulated streams in other regions or even to other lotic systems in the Rocky Mountains. The proliferation of dams necessitates a fuller understanding of the effects of stream regulation and provides a setting for testing and developing basic theories of stream ecology.

Acknowledgments — The authors wish to thank Dr J. A. Stanford, North Texas State University, for reading the manuscript.

ANDERSON, N. H., AND J. R. SEDELL. 1979. Detritus processing by macroinvertebrates in streams. Annu. Rev. Entomol. 24: 351–377.

BENFIELD, E. F., D. S. JONES, AND M. F. PATTERSON. 1977. Leaf pack processing in a pastureland stream. Oikos 29: 99–103.

GELROTH, J. V., AND G. R. MARZOLF. 1978. Primary production and leaf-litter decomposition in natural and channelized portions of a Kansas stream. Amer. Midl. Nat. 99: 238–243.

HART, S. D., AND R. P. HOWMILLER. 1975. Studies on the decomposition of allochthonous detritus in two southern California streams. Verh. Int. Verein. Limnol. 19: 1665–1674.

MERRITT, R. W., AND K. W. CUMMINS. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

PETERSEN, R. C., AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. Freshwater Biol. 4: 343–368.

REICE, S. R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. Ecology 55: 1271–1282.

REICE, S. R. 1977. The role of animal associations and current velocity in sediment specific leaf litter decomposition. Oikos 29: 357–365.

SEDELL, J. R., F. J. TRISKA, AND N. S. TRISKA. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Verh. Int. Verein. Limnol. 19: 1617–1627.

SHORT, R. A., S. P. CANTON, AND J. V. WARD. 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. Ecology. (In press)

TRISKA, F. J., AND J. R. SEDELL. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology 57: 783–792.

WARD, J. V. 1976a. Comparative limnology of differentially regulated sections of a Colorado mountain river. Arch. Hydrobiol. 78: 319–342.

1976b. Effects of thermal constancy and seasonal temperature displacement on community structure of stream macroinvertebrates, p. 302–307. *In* G. W. Esch and R. W. McFarlane [ed.], Thermal ecology II, ERDA Symposium Series (CONF-740425).

WARD, J. V., AND R. A. SHORT. 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, U.S.A. Verh. Int. Verein. Limnol. 20: 1382–1387.

WARD, J. V., AND J. A. Stanford [ed.] 1979. The ecology of regulated streams. Plenum Publishing Corp., New York, N.Y. (In press)

A Motion for the Retirement of the Von Bertalanffy Function

DEREK A. ROFF

Department of Fisheries and Oceans, Fisheries and Marine Service, P.O. Box 5667, St. John's, Nfld. A1C 5X1

ROFF, D. A. 1980. A motion for the retirement of the von Bertalanffy function. Can. J. Fish. Aquat. Sci. 37: 127–129.

The reasons for the continued use of the von Bertalanffy equation are examined. It is suggested that these reasons are insufficient to overcome the drawbacks of this function and alternative procedures are recommended.

Key words: von Bertalanffy, growth, yield per recruit

ROFF, D. A. 1980. A motion for the retirement of the von Bertalanffy function. Can. J. Fish. Aquat. Sci. 37: 127–129.

Nous analysons les raisons pour lesquelles on continue d'utiliser l'équation de von Bertalanffy. Nous suggérons que ces raisons sont insuffisantes pour l'emporter sur les désavantages de cette fonction, et nous recommandons d'autres méthodes.

Received June 18, 1979
Accepted October 4, 1979

Reçu le 18 juin 1979
Accepté le 4 octobre 1979

ONE of the most ubiquitous equations in the fisheries literature is the von Bertalanffy function. Historically it gained wide currency because it claimed to be developed from bioenergetic principles. However, as pointed out by several authors (Parker and Larkin 1959; Paloheimo and Dickie 1964; Ursin 1967) this equation, from a bioenergetic perspective, is at best a special case and at worst nonsense (Knight 1968). Given that the equation can no longer be justified on the grounds upon which it was developed, why has it remained so much in use? In this note I examine the reasons for this and suggest that they do not outweigh the disadvantages of the von Bertalanffy equation.

Probably the most general reason for the continued use of this equation is that it is a convenient statistical description of the data. But is it so convenient? There are principally two statistical reasons for selecting a particular equation: firstly, the equation may be very flexible and fit a wide range of data and secondly the equation may be easily fitted to the data. The first is certainly true of the von Bertalanffy function but the second is decidely not true, as testified by the recurrence of papers providing methods of fitting it and other

Printed in Canada (J5680)
Imprimé au Canada (J5680)