Multiple Trophic Levels of a Forest Stream Linked to Terrestrial Litter Inputs

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The importance of terrestrial-aquatic linkages was evaluated by a large-scale, 3-year exclusion of terrestrial leaf litter inputs to a forest stream. Exclusion of leaf litter had a strong bottom-up effect that was propagated through detritivores to predators. Most invertebrate taxa in the predominant habitat declined in either abundance, biomass, or both, compared with taxa in a nearby reference stream. However, fauna in moss habitats changed little, indicating that different food webs exist in habitats of different geomorphology. Thus, the ecosystem-level consequences of excluding detrital inputs to an ecosystem were demonstrated. Inputs of riparian detritus are essential for conservation or restoration of diverse stream food webs.

Detritus, or dead organic matter (*1*), is the major carbon pathway in most ecosystems: 70 to 90% of all primary production eventually enters the detrital food web (*2*). The addition of detritus to food webs complicates classical plant-herbivore-predator relationships (*3*). Indeed, in most headwater streams draining forests in eastern North America, inputs of detritus from the surrounding forest exceed within-stream primary production (*4*). One of the basic tenets of stream ecology for more than two decades has been the importance of terrestrial-aquatic linkages (*5*). Although details about linkages between detritivores and detritus processing in streams are well known (*2*, *6*, *7*), there is little direct evidence supporting the importance of terrestrial detrital inputs and ecosystem productivity (*8*) and it is limited to short-term studies in artificial channels (*9*). It has also been suggested that several generations of consumers are required to detect responses to detrital manipulations (*10*). We studied the role of detritus in ecosystem productivity by excluding inputs of terrestrial litter to a 180-m-long headwater stream, using an overhead canopy and a lateral fence for 3 years (*11*). We evaluated the impact of the basal resource (terrestrial litter inputs) in this forest stream on abundance, biomass, and production of animals.

In addition to examining numerical abundances of populations, we calculated secondary production as the flow (or flux) of mass · area^{-1} · time^{-1}, which incorporates abundance, biomass, individual growth rates, survivorship, and development times into a single metric (*12*). Production provides the best measure of the relationship of animals to energy flow in ecosystems (*12*, *13*). Benthic animal abundance and biomass were sampled from two distinct habitats: mixed substrates and moss-covered bedrock (*14*). We used randomized intervention analysis (*15*) to compare multiyear differences of animal abundance and biomass between reference and treatment streams.

As a result of litter exclusion, we observed major changes in abundance, biomass, and production of the invertebrate fauna in the treated stream. On the basis of modes of feeding [functional feeding groups (FFG) (*16*)], animal populations in the two stream habitats (*14*) responded very differently to litter exclusion (Table 1). Significant changes occurred in abundance or biomass of large- and fine-particle-feeding detritivores (shredders and collectors, respectively) and predators in the dominant mixed substrate habitats (cobble, pebble, and gravel-sand). However, on moss-covered bedrock, there were no significant differences between streams for abundance or biomass of animals belonging to any FFG.

Seventeen of the 29 major taxa in the

Table 1. Average monthly abundance (number/m^2) and biomass (mg AFDM/m^2) ± 1 SD in mixed substrate and bedrock outcrop habitats of the reference and litter-exclusion stream before treatment (pretreatment period was September 1992 to August 1993, n = 12) and during treatment (litter exclusion period was September 1993 to August 1996, n = 36). Abundance and biomass in the mixed substrates of the litter-excluded stream declined with each successive year of treatment. 1° consumers, primary consumers; Invert. pred., invertebrate predators; Ref., reference stream; Excl., exclusion stream.

Trophic group	Stream	Abundance ± SD		Biomass ± SD	
		Pretreatment	Posttreatment	Pretreatment	Posttreatment
		Mixed substrates			
Scrapers	Ref.	44 ± 45	17 ± 34	2 ± 3	3 ± 6
	Excl.	562 ± 469	367 ± 314	6 ± 4	6 ± 7
Shredders	Ref.	1360 ± 847	2951 ± 1884	700 ± 306	764 ± 472
	Excl.	954 ± 588	554 ± 431**	401 ± 338	234 ± 250†
Gatherers	Ref.	53,733 ± 24,072	81,453 ± 41,703	339 ± 214	270 ± 100
	Excl.	30,940 ± 14,431	18,019 ± 9874**	158 ± 104	74 ± 37*
Filterers	Ref.	288 ± 337	414 ± 398	102 ± 93	38 ± 25
	Excl.	323 ± 546	188 ± 233	35 ± 32	27 ± 24
1° consumers	Ref.	55,425 ± 24,446	84,835 ± 42,617	1143 ± 404	1075 ± 501
	Excl.	32,779 ± 14,927	19,128 ± 10,237**	600 ± 376	341 ± 257*
Invert. pred.	Ref.	6827 ± 2618	9519 ± 4649	672 ± 322	943 ± 352
	Excl.	4892 ± 2486	2883 ± 2121**	403 ± 259	179 ± 140**
Salamanders	Ref.	5 ± 10	11 ± 13	58 ± 97	103 ± 140
	Excl.	4 ± 6	1 ± 2*	29 ± 35	5 ± 19*
		Bedrock substrates			
Scrapers	Ref.	174 ± 162	239 ± 266	59 ± 73	17 ± 16
	Excl.	262 ± 195	383 ± 537	36 ± 54	25 ± 47
Shredders	Ref.	578 ± 367	901 ± 784	82 ± 63	73 ± 86
	Excl.	622 ± 605	608 ± 542	52 ± 53	40 ± 43
Gatherers	Ref.	15,554 ± 7822	11,929 ± 7509	186 ± 176	93 ± 88
	Excl.	12,191 ± 8974	11,613 ± 9,590	90 ± 50	62 ± 47
Filterers	Ref.	1127 ± 1446	1181 ± 1455	429 ± 380	241 ± 277
	Excl.	906 ± 764	715 ± 1073	337 ± 334	136 ± 115
1° consumers	Ref.	17,433 ± 8363	14,250 ± 7566	756 ± 565	424 ± 290
	Excl.	13,981 ± 9353	13,319 ± 10,665	515 ± 395	263 ± 166
Invert. pred.	Ref.	3043 ± 1437	2666 ± 1471	113 ± 64	59 ± 42
	Excl.	2532 ± 1038	2055 ± 1374	97 ± 94	42 ± 46
Salamanders	Ref.	0 ± 0	1 ± 4	0 ± 0	17 ± 67
	Excl.	0 ± 0	1 ± 5	0 ± 0	12 ± 73

Probability levels for RIA of change between reference and treatment stream abundance and biomass [log (x + 1) transformed] are: *$P < 0.05$ and **$P < 0.001$. †RIA, $P = 0.069$ for shredder biomass.

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mixed substrates, constituting 93 to 97% of the benthic production in the reference and treatment streams, displayed significant reductions in either abundance or biomass, or both, during the period of exclusion (Table 2). Several invertebrates that failed to show significant decreases are those known to feed on woody debris or organic particles buried in stream sediments (*17*), which were present throughout the 3-year exclusion period (*18*).

Patterns of secondary production for mixed substrates exhibited diverging trends in the litter exclusion and reference streams (Fig. 1), as observed for abundance and biomass. In contrast, production on moss-covered bedrock substrates in the two streams followed similar patterns throughout the 4-year period. Despite the close proximity of mixed substrate and bedrock habitats, our results indicate that different food webs occur within these different habitats. These results also show that geomorphology, that is, the physical nature of the substratum, affects resource availability to consumers. Fauna on the steep-gradient, moss-covered bedrock habitats rely on small particles transported by streamflow or trapped within the moss (*19*). Fine organic particles stored within moss-covered bedrock habitats did not decrease during the 3 years of the study, and total export of fine particles from the exclusion stream did not decrease until the third year (*20*). These findings indicate that this food resource was largely maintained throughout the observation period. Thus, the bedrock outcrop community is less directly dependent on leaf litter than the community found in mixed substrates (Table 1 and Fig. 1).

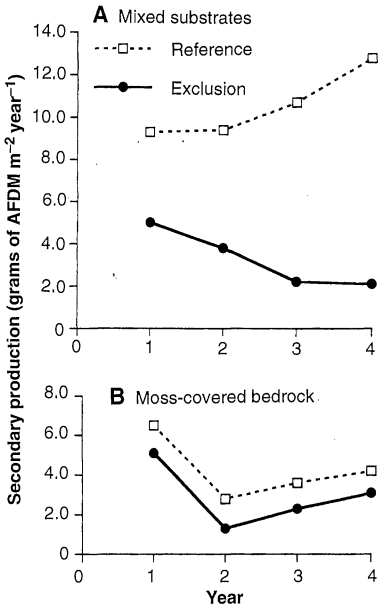

Fig. 1. Annual secondary productivity of benthic invertebrates. Year 1 was the pretreatment year followed by 3 years of litter exclusion. Data are shown for (**A**) mixed substrate habitats in the reference and litter exclusion streams and (**B**) moss-covered bedrock outcrop habitats in the same streams.

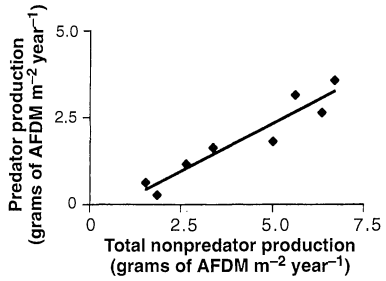

Fig. 2. Relationship between nonpredator invertebrate production and that of invertebrate predators in mixed substrates of the litter exclusion stream. Each point represents an annual value. Four of these years represent prior studies (*22*), and the other 4 years are pretreatment and 3 years of exclusion (three points in lower left).

Table 2. RIA probabilities of change in benthic populations between reference and treatment stream abundance and biomass [log (x + 1) transformed data] for specific invertebrate taxa (organized by FFG) for mixed substrates after 3 years of litter exclusion (n = 48). Insect orders are as follows: D, Diptera; E, Ephemeroptera; NI, noninsect; O, Odonata; P, Plecoptera; and T, Trichoptera. *Diplectrona modesta* was the only taxon that increased in the treatment stream relative to the reference stream.

Taxon	Order	Abundance	Biomass
Shredder			
Peltoperlidae	P	ns	*
Leuctra spp.	P	*	**
Lepidostoma spp.	T	***	***
Pycnopsyche spp.	T	*	*
Fattigia pele	T	ns	ns
Tipula spp.	D	ns	ns
Molophilus spp.	D	ns	ns
Lipsothrix sp.	D	ns	ns
Collector-gatherer			
Nematoda	NI	*	*
Oligochaeta	NI	ns	ns
Copepoda	NI	***	***
Paraleptophlebia sp.	E	ns	ns
Stenonema spp.†	E	***	***
Lype diversa	T	ns	ns
Sciaridae (*Bradysia* sp.)	D	ns	ns
Chironomidae‡	D	***	**
Collector-filterer			
Diplectrona modesta	T	*	*
Parapsyche cardis	T	ns	ns
Predator			
Lanthus sp.	O	***	***
Cordulegaster sp.	O	**	**
Beloneuria sp.	P	*	**
Isoperla spp.	P	ns	ns
Sweltsa lateralis	P	ns	ns
Rhyacophila spp.	T	ns	*
Tanypodinae	D	***	**
Ceratopogonidae	D	***	**
Hexatoma spp.	D	**	**
Dicranota spp.	D	ns	ns
Pedicia sp.	D	**	**

Probability levels are: *P < 0.05, **P < 0.01, ***P < 0.001, and ns, no significant difference between streams. †FFG based on gut content analysis. ‡Non-Tanypodinae.

Predators also displayed strong reductions in the exclusion stream, following the trend of total primary consumers (Tables 1 and 2). Invertebrate predator production in fishless, headwater streams at Coweeta usually represents about 24 to 33% of total invertebrate production (*14*). Predator production declined in the treatment stream during each successive year of treatment, which suggests bottom-up effects of exclusion. Some common prey also decreased in abundance and biomass during exclusion, such as midge larvae (Order: Diptera) and copepods, both of which have high growth rates in these streams (*21*). We found a strong positive regression between total nonpredator and predator production in the litter exclusion stream (Fig. 2) (*22*). Furthermore, the slope (0.36) of the relationship between total invertebrate production and that of predators is remarkably similar to values for efficiency of conversion of ingested food by invertebrate predators (*23*) and suggests that predators are food-limited in the exclusion stream. These data imply that invertebrate predators in these headwater streams consume most of the invertebrate production, suggesting that invertebrate predators may exert top-down effects on their prey. Over the range of productivity measured, the close agreement between predators and prey in Fig. 2 is more consistent with models based on co-limitation by resources and predators (*24*) rather than top-down models (*25*). Others (*3*, *26*) have suggested that top-down effects occur primarily in simple plant-herbivore-predator food chains and are not observed in speciose communities with an externally subsidized detrital energy base. However, in addition to the bottom-up effects demonstrated by litter exclusion, top-down effects appear to be important in this detrital-based stream as in other systems (*27*).

Multiyear manipulations of entire ecosystems are important tools to assess environmental change and the factors controlling ecosystem-level processes (*28*). Bottom-up effects have been studied by adding nutrients to lakes (*29*) and streams (*30*), but ecosystem-level studies examining the effects of resource reduction on communities are rare. Yet, many natural and anthropogenic disturbances reduce terrestrial litter inputs to streams, for ex-

ample, fire (*31*), logging (*32*), land-use change (*33*), channelization (*34*), and grazing (*35*). However, these activities often induce multiple effects that confound analyses of biotic responses to disturbance: altered hydrology; enhanced sediment, nutrient, and solar inputs; and shifts in the relative importance of detrital inputs and stream primary production. These diverse direct and indirect effects complicate analyses of animal community response to disturbance. We demonstrated the consequences of disrupting leaf litter inputs to aquatic community structure and productivity, while minimizing the indirect effects that occur with more complex disturbances.

Experimental exclusion of leaf litter has demonstrated a strong effect of detrital resource reduction propagated through detritivores to predators. Our study provides experimental evidence of the importance of terrestrial-aquatic ecotones to aquatic diversity and productivity. Human actions have resulted in worldwide loss and degradation of riparian zones (*36*), thereby altering the supply of leaf litter to stream ecosystems. Maintaining or reestablishing these inputs of riparian detritus is an essential element of conservation or restoration of diverse riverine food webs.

REFERENCES AND NOTES

1. J. D. Allan, *Stream Ecology* (Chapman and Hall, London, 1995).
2. R. V. O'Neill and D. A. Reichle, in *Forests: Fresh Perspectives from Ecosystem Analysis*, R. H. Waring, Ed. (Oregon State Univ. Press, Corvallis, OR, 1980), pp. 11–26; L. R. Pomeroy, in *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*, J. Cole *et al.*, Eds. (Springer-Verlag, New York, 1991), pp. 97–119; R. G. Wetzel and A. K. Ward, in (*7*), pp. 354–369.
3. G. A. Polis, *Aust. J. Ecol.* **19**, 121 (1994); _____ and D. R. Strong, *Am. Nat.* **147**, 813 (1996).
4. J. R. Webster *et al.*, in *River and Stream Ecosystems*, C. E. Cushing *et al.*, Eds. (Elsevier, Amsterdam, 1995), pp. 117–187.
5. K. W. Cummins, *Bioscience* **24**, 631 (1974); H. B. N. Hynes, *Verh. Int. Ver. Theor. Angew. Limnol.* **19**, 1 (1975).
6. N. H. Anderson and J. R. Sedell, *Annu. Rev. Entomol.* **24**, 351 (1979); J. R. Webster and E. F. Benfield, *Annu. Rev. Ecol. Syst.* **17**, 567 (1986); C. E. Cushing *et al.*, Eds., *River and Stream Ecosystems* (Elsevier, Amsterdam, 1995); J. B. Wallace and J. R. Webster, *Annu. Rev. Entomol.* **41**, 115 (1996).
7. P. Calow and G. E. Petts, Eds., *The Rivers Handbook* (Blackwell, Oxford, 1992).
8. C. P. Hawkins and J. A. MacMahon, *Annu. Rev. Entomol.* **34**, 423 (1989).
9. J. S. Richardson, *Ecology* **72**, 873 (1991).
10. _____ and W. E. Neill, *Can. J. Fish. Aquat. Sci.* **48**, 776 (1991).
11. After a year of pretreatment study on Catchment 55 and a nearby reference stream draining Catchment 53, a litter exclusion canopy was constructed in August 1993 on Catchment 55 (treatment stream) at the Coweeta Hydrologic Laboratory (35°03′N, 83°25′W) of the U.S. Forest Service in western North Carolina. The canopy is 180 m long and covers the entire bankful width of the stream from the flume at the base of the catchment to the headwater spring seep. The canopy is open at the sides and below a dense rhododendron understory and overstory trees. The canopy is constructed of gill netting with 1.2-cm mesh openings. Light attenuation by the canopy is <1%. Material landing on the canopy was removed at regular intervals with a leaf blower. A lateral movement fence on each bank, 45 cm high, with 1-cm mesh, prevented lateral inputs of litter. During the 3 years of litter exclusion, direct litterfall traps outside the canopy received a total of 1.12 kg ash-free dry mass (AFDM)/m^2 of leaf litter, whereas those traps below the canopy received 0.05 kg/m^2 (equal to 95.2% exclusion efficiency). Lateral movement traps, located outside and inside of the lateral movement fence, indicated a similar efficiency (95.0%). Primary production in the headwater streams at Coweeta is very low (4).
12. A. C. Benke, *Verh. Int. Ver. Theor. Angew. Limnol.* **25**, 15 (1993).
13. A. D. Huryn, *Limnol. Oceanogr.* **41**, 243 (1996); A. C. Benke and J. B. Wallace, *Ecology* **78**, 1132 (1997).
14. G. J. Lugthart and J. B. Wallace, *J. North Am. Benthol. Soc.* **11**, 138 (1992). Benthic sampling methods were as follows: three samples in bedrock outcrops and four samples in mixed substrates were collected each month in each stream. Processing of samples and methods used to measure secondary production followed procedures described by Lugthart and Wallace. Average stream widths (reference stream, 1.1 m and treatment stream, 1.4 m) and substrate were estimated at 1-m intervals for both streams. The exclusion stream has 87% mixed substrates (cobble, pebble, and depositional) and 13% moss-covered bedrock. The reference stream substratum is 73% mixed substrates and 27% moss-covered bedrock. Production of aquatic vertebrate predators (salamanders) represents <1 to 5% of total secondary production in these streams.
15. S. R. Carpenter *et al.*, *Ecology* **70**, 1142 (1989). Randomized intervention analysis (RIA) requires a pretreatment period of study for both reference and treatment sites. This is followed by a treatment period in which intersite differences are compared with pretreatment differences. Significant statistical differences do not imply that results were due to treatment, only that significant changes occurred between streams. RIAs were calculated only on abundance and biomass from monthly samples (n = 48). Production was calculated for each taxon as an annual value. Power analysis [C. W. Osenberg *et al.*, in *Detecting Ecological Impacts*, R. J. Schmitt and C. W. Osenberg, Eds. (Academic Press, San Diego, 1996), pp. 83–108] on statistically nonsignificant results indicated that small effect sizes and not increased variability were responsible for the nonsignificant differences.
16. R.W. Merritt and K. W. Cummins, Eds. *Aquatic Insects of North America* (Kendall-Hunt, Dubuque, IA, 1996).
17. Examples of taxa that feed on material buried in the substratum are sericostomatid caddisfly larvae, *Fattigia* [R. Wagner, *Hydrobiologia* **224**, 65 (1991)]; Diptera, *Molophilus* (*16*); and Oligochaeta. We extracted gut contents of larvae and measured projected areas of various food resources by using a compound microscope, camera lucida, and digitizing tablet [J. B. Wallace *et al.*, *Arch. Hydrobiol. Suppl.* **74**, 423 (1987)]. Guts of some specimens contained >60% woody tissue. Others have reported woody tissue as common in guts of insects, such as *Lipsothrix* [T. L. Dudley and N. H. Anderson, *Freshwater Biol.* **17**, 437 (1987)] and *Paraleptophlebia*, *Tipula*, and Sciaridae [C. R. D. Pereira *et al.*, *Melanderia* **39**, 23 (1982)].
18. After 3 years of litter exclusion (September 1996), we removed, weighed, and ashed (muffle furnace at ~500°C) 337 kg AFDM of small wood (<10 cm in diameter) from the exclusion stream. The wood we removed, as well as remaining large wood (>10 cm in diameter), and fine organic particles (<1 mm in diameter) stored within the stream bed (ranging from 1.05 kg AFDM/m^2 during pretreatment to 0.52 kg AFDM/m^2 during the third year of exclusion) constituted a large residual source of terrestrially derived organic matter available to invertebrates throughout the study. Furthermore, inputs of groundwater dissolved organic carbon were not curtailed.
19. A. D. Huryn and J. B. Wallace, *Ecology* **68**, 1932 (1987); *Freshwater Biol.* **20**, 141 (1988).
20. Benthic organic matter stored within the moss-covered bedrock substrate ranged from 36.9 (pretreatment) to 42.6 g AFDM/m^2 during 3 years of exclusion. Export of fine particles has been measured continuously in both streams since early 1985 [T. F. Cuffney and J. B. Wallace, *Can. J. Fish. Aquat. Sci.* **45**, 2010 (1988)]. Fine organic particle export in the exclusion stream did not decrease relative to the reference stream until the third year of exclusion (J. B.Wallace *et al.*, unpublished data).
21. E. C. O'Doherty, *Limnol. Oceanogr.* **30**, 554 (1985); A. D. Huryn, *ibid.* **35**, 339 (1990).
22. Data shown in Fig. 2 include 4 years of annual production measurements made prior to the present study (1985, 1986, 1989, and 1990) and are represented by the four points in upper right of the graph [(*14*); M. R. Whiles and J. B. Wallace, *Can. J. Fish. Aquat. Sci.* **52**, 2402 (1995)]. During "normal" years, streams experience natural variation as storms remove leaf litter from the wetted channel. There is a strong relationship between annual invertebrate productivity in mixed substrates and standing crop of leaf litter (r^2 = 0.90, $P < 0.001$). The axes of nonpredator production with total predators are independent (slope = 0.55, r^2 = 0.90, $P < 0.001$).
23. A plot of total invertebrate production with total predator production (not shown, r^2 = 0.96) is not independent; however, inclusion of predators in both axes (since predators also eat other predators in our stream) yields a slope (0.36) that is in close agreement with general bioenergetic efficiencies (production/ingestion) reported for invertebrate predators (33 to 39%) [F. Slansky Jr. and J. M. Scriber, *Bull. Entomol. Soc. Am.* **28**, 43 (1982)].
24. M. E. Power, *Ecology* **73**, 733 (1992).
25. L. Oksanen *et al.*, *Am. Nat.* **118**, 240 (1981); see also table 1 and figure 3 in (*24*).
26. D. R. Strong, *Ecology* **73**, 747 (1992).
27. M. E. Power, *Science* **250**, 811 (1990); M. D. Hunter and P. W. Price, *Ecology* **73**, 724 (1992); S. R. Carpenter and J. F. Kitchell, *The Trophic Cascade in Lakes* (Cambridge Univ. Press, New York, 1993); P. C. de Ruiter, A.-M. Neutel, J. C. Moore, *Science* **269**, 1257 (1995).
28. S. R. Carpenter, S. W. Chisholm, C. J. Krebs, D. W. Schindler, R. F. Wright, *Science* **269**, 324 (1995).
29. D. W. Schindler *et al.*, *J. Fish. Res. Board Can.* **35**, 190 (1978); W. T. Edmondson and J. T. Lehman, *Limnol. Oceanogr.* **26**, 1 (1981).
30. J. W. Elwood *et al.*, *Ecology* **62**, 146 (1981); B. J. Peterson *et al.*, *Science* **229**, 1383 (1985); A. D. Rosemond *et al.*, *Ecology* **74**, 1264 (1993).
31. G. A. Meyer *et al.*, *Nature* **357**, 147 (1992); G. W. Minshall *et al.*, *Great Basin Nat.* **55**, 193 (1995).
32. F. H. Bormann and G. E. Likens, *Pattern and Process in a Forested Ecosystem* (Springer-Verlag, New York, 1979); J. R. Webster *et al.*, in *Stream Ecology*, J. R. Barnes and G. W. Minshall, Eds. (Plenum, New York, 1983), pp. 355–395; W. T. Swank and D. A. Crossley, Eds., *Forest Hydrology and Ecology at Coweeta* (Springer-Verlag, New York, 1988).
33. B. W. Sweeney, *Proc. Acad. Nat. Sci. Phila.* **144**, 291 (1993); R. C. Wissmar *et al.*, *Northwest Sci.* **68**, 1 (special issue 1994); J. S. Harding and M. J. Winterbourn, *N.Z. J. Mar. Freshwater Res.* **29**, 479 (1995).
34. J. M. Quinn *et al.*, *N.Z. J. Mar. Freshwater Res.* **26**, 259 (1992).
35. W. H. Rickard and C. E. Cushing, *J. Range Manage.* **35**, 360 (1982); C. Armour *et al.*, *Fisheries* **19**, 9 (1994).
36. B. L. Swift, *Water Resour. Bull.* **20**, 223 (1984); S. V. Gregory *et al.*, *Bioscience* **41**, 540 (1991); C. Nilsson *et al.*, *Science* **276**, 798 (1997).

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