

A SURVEY OF AQUATIC INSECTS ASSOCIATED WITH
WOOD DEBRIS IN NEW ZEALAND STREAMS

N. H. ANDERSON

Department of Entomology, Oregon State University,
Corvallis, Oregon 97331, U.S.A.

ABSTRACT

The wood-associated aquatic invertebrate fauna was investigated by surveying about 70 sites representing a range of stream habitats in both the South and North Islands of New Zealand. Compared with sites in Oregon, U.S.A. there was less wood debris in New Zealand streams and also fewer wood-associated invertebrates. However, wood is utilized by the New Zealand fauna in similar ways to that found in Oregon. The impact of semi-aquatic, rather than fully aquatic species, on wood degradation seems to be relatively greater in New Zealand. Tipulid larvae, especially *Limonia nigrescens*, are the dominant wood processors of saturated wood. Amongst the broad spectrum of insects collected from wood in streams, those most closely associated with this habitat were: Plecoptera - *Austroperla cyrene*; Ephemeroptera - *Zephlebia*; Trichoptera - *Triplectides obsoleta* and *Pycnocentria sylvestris*; Coleoptera - Helodidae larvae; Chironomidae - *Harrisius pallidus* and an undescribed genus of Orthocladiinae.

KEYWORDS: invertebrate, aquatic insects, wood debris, streams, wood degradation, New Zealand, Oregon, U.S.A.

INTRODUCTION

The importance of terrestrial inputs as a food base for stream organisms has long been recognized (e.g. Thienemann 1912), but it is only in the past two decades that the subject has been actively investigated. Anderson and Sedell (1979) reviewed the literature on inputs of large particulate organic matter from the surrounding watershed and its degradation and utilization by the stream biota. Most studies are from Europe and North America and emphasize the importance of leaf litter, especially the autumnal leaf fall from deciduous trees. Wood debris may be the major component of organic material in forested streams, but

compared with leaf litter, the study of rates of degradation and the mechanisms of breakdown in water have received little attention (Triska and Cromack 1980).

According to Triska and Cromack (1980), the largest accumulations of wood debris in North American streams occur in the coniferous forests of the west coast; in old-growth Douglas fir (*Pseudotsuga menziesii*) stands, they record 25-40 kg/m², and from 45-80 kg/m² in streams in the redwoods (*Sequoia sempervirens*) of northern California. They suggest that the biota of streams in forested areas evolved in systems where wood debris played a far larger role than it does today and that wood debris has been removed in many parts of the world before man has fully understood its role.

A long-term study of the role of aquatic invertebrates on the processing of wood debris in Oregon streams was begun in 1975. There is a characteristic fauna associated with wood debris but its biomass is much lower than that found in leaf debris (Anderson et al. 1978; Dudley and Anderson 1982). This difference is related to the low food quality of wood. It is very low in nitrogen (C:N ratio 300-1300:1) and contains about 80% lignin and cellulose which are only slowly degraded by microbes.

In 1979 a comparison of the wood-associated fauna of New Zealand streams with that in Oregon was undertaken. The comparison is appropriate because of latitudinal and climatic similarities, while differences could be expected to occur because of the unique flora and fauna of New Zealand. The specific objective was to survey the wood-associated invertebrates to determine whether abundance, diversity and utilization of this substrate exhibited similar patterns to that which obtain in Oregon streams.

SURVEY PROCEDURES AND METHODS

Invertebrates were collected from wood debris at about 70 sites. These included a variety of stream types and topographical areas in both the South and North Islands (Fig. 1). To obtain a good cross-section of the fauna, the survey included streams that varied with respect to stream order, gradient, substrate, and abundance of wood debris. Riparian vegetation included sites with beech (*Nothofagus*), mixed podocarps (*Podocarpus* and *Dacrydium*), regrowth scrub and tree ferns (*Cyathea* and *Dicksonia*), and exotics, including willow (*Salix*), alder (*Alnus*), and plantations of pine (*Pinus*) and Douglas Fir (*Pseudotsuga menziesii*).

Collecting was concentrated in small streams as wood debris is most prevalent where stream power is insufficient to dislodge the wood. However, it was difficult to find undisturbed watersheds because of their remoteness from Christchurch and also because road access to such areas is very limited. The most extensive collections were from: (1) the Arthur's Pass area, especially Middle Bush Stream, and a tributary to the Andrews Stream (see Winterbourn (1977)); (2) brown water streams along the

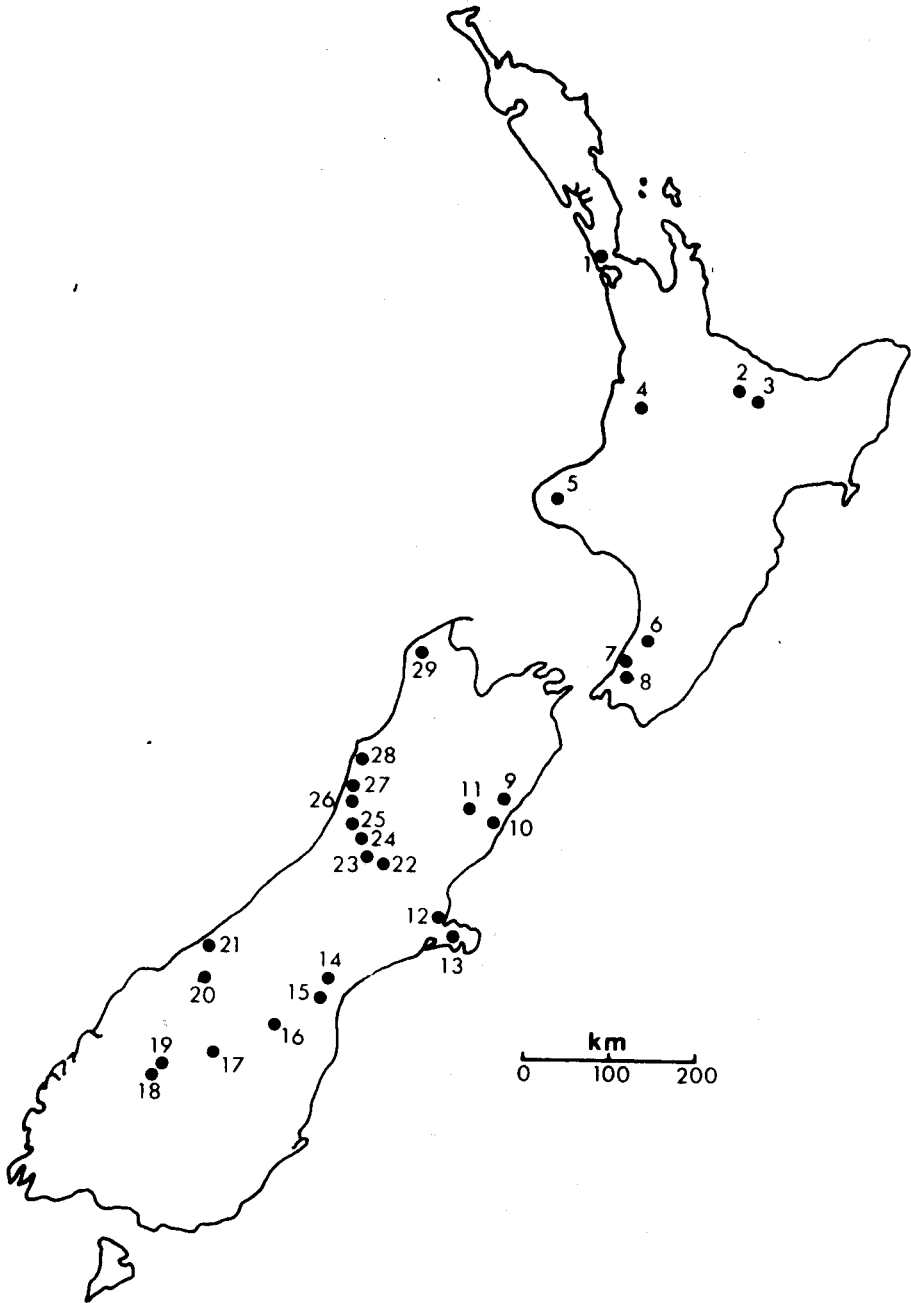


Fig. 1. Locations of streams from which wood and associated invertebrates were collected in 1979. For key to sites see Appendix.

west coast between Greymouth and Westport; and (3) the Kaituna River on Banks Peninsula. The largest collection on the North Island was from the Waitakere River site of Towns (1981).

Wood debris was examined for invertebrates in the field, or returned to the laboratory where it was sprayed with water to remove the fauna. If there was evidence of burrowing into the wood, the surface was pared away with a knife to collect the larvae, or the material was held in a container to obtain adults at emergence. The semi-aquatic fauna is more important than the truly aquatic community in effecting wood degradation (Dudley and Anderson 1982). Thus, sodden wood from the stream edge was collected as well as that occurring directly in the stream.

Gut contents were examined from over 100 specimens of surface-associated taxa to determine whether they had ingested wood particles. Specimens used for dissection were collected from 15 sites. The primary criterion for use in gut analysis was availability of adequate well-preserved individuals. The gut was removed and the food bolus dispersed in water. The material was then filtered through a Millipore filter. The filter paper was cleared with light immersion oil, mounted on a slide and examined with a compound microscope. Most wood fragments could be recognized and distinguished from other detritus by the presence of lignified fibrous tissue, spiral thickenings, pits, and entire tracheids or parts thereof. Species collected below the wood surface were generally not dissected as their guts were expected to contain wood.

A limited amount of laboratory rearing was attempted in a constant temperature cabinet and aquarium room at 15-16°C. Insects were maintained in plastic boxes or petri dishes with wood from the field site where they were collected. Water level was kept low so that part of the wood was exposed to the air. Collections of faeces (including fine particles produced by feeding or other activity) were obtained by gentle washing of the wood surface and subsequent concentration by filtration. The preliminary nature of the laboratory studies is emphasized. The objectives were to observe feeding behaviour, especially the potential for scraping, gouging or boring into wood, and to obtain an index of the amount of fine particles produced by feeding activity.

RESULTS AND DISCUSSION

This survey indicated that most New Zealand streams contain very little wood debris in comparison with Oregon streams. Winterbourn et al. (1981) attribute this paucity of in-channel wood to the unstable nature of the channels and their poor retention characteristics. In areas where small low-gradient streams occur, the forests have largely been cleared and riparian vegetation is relatively sparse. Thus, in the majority of streams examined, the role of wood debris was quite limited either as a habitat or as a food base for aquatic invertebrates.

At Cass, both the tributary to the Andrews Stream and the Middle Bush Stream were sites with relatively stable channels and some wood control of channel morphology. The sites may be representative of undisturbed conditions in beech forests. Wood debris was abundant and occurred in all rot classes from firm, newly fallen wood to pieces in advanced stages of decay. The organic fines in drop zones of Middle Bush contained a high proportion of wood-derived material which had been produced either by physical abrasion or biological activity. About 40 taxa were collected from wood at the Cass sites, and most have been recorded from detritus and stones in Middle Bush Stream (Winterbourn 1978). This suggests that most taxa were only opportunistically associated with wood which is used primarily as habitat. However, as indicated in the discussion of taxa collected in the full survey, there was also a xylophilous component which exploited this habitat in several ways.

Taxa Associated With Wood

EPHEMEROPTERA.

The common mayflies on wood debris were species of *Zephlebia*, *Coloburiscus* and *Deleatidium*, while a few *Nesameletus* also were collected. With the possible exception of *Zephlebia*, mayfly larvae appeared to have a minimal impact on wood degradation. Wood particles were found in one of five guts of *Zephlebia* examined and three others contained fungal mycelia which were probably scraped from wood surfaces.

PLECOPTERA.

Several species of stoneflies were common or abundant on wood debris, especially in mountain streams. All families were represented including the predaceous eustheniid, *Stenoperla prasina*. Gripopterigids (*Acroperla*, *Zelandobius*, *Zelandoperla*) or notonemourids (*Spaniocerca*, *Halticoperla*) were the most abundant, but the large austroperlid, *Austroperla cyrene*, was probably the species most closely associated with wood debris. *A. cyrene* is reported as a wood feeder both as larvae and adults (Winterbourn 1977). Three of six larvae dissected in this study contained wood fragments. Members of the other families (except Eustheniidae) are general detritivores and with their scraping mode of feeding they probably ingest some of the soft superficial layers of decayed wood. However, the only species in which wood was positively identified in gut contents was *Spaniocerca zelandica* (three of five specimens).

TRICHOPTERA.

Larvae of the free-living Hydrobiosidae and the net-spinning or retreat-building Polycentropodidae, Hydropsychidae and Philopotamidae were commonly collected from wood debris. These taxa are predators or filter feeders so they are considered to be only opportunistically associated and would have little effect on wood degradation. Larvae of the hydropsychid, *Aoteapsyche*, collected in the Waitakere River, had gouged

depressions in sunken logs for their retreats so they did cause some particle-size reduction of the substrate.

Case-making caddisflies are a major component of the Oregon xylophilous fauna, so comparable examples were looked for within the New Zealand fauna. Families that are common in small New Zealand forest streams and included species frequently associated with wood debris were the detritivorous Leptoceridae, Conoesucidae, Oeconesidae, and the predaceous Philorheithridae. As well as a larval substrate, wood is used as a pupation site and by adults for oviposition. Egg masses of *Philorheithrus agilis* and *Oeconesus maori* were collected from saturated wood, and *Zelandopsyche ingens* also uses wood as an oviposition substrate (Winterbourn 1978). *Olinga feredayi* and *Pycnocentria evecta* were the common species whose pupae were attached to wood surfaces but *P. agilis* and *Pycnocentrodes* sp. were also found on wood. Prepupae and pupae of the leptocerids, *Triplectides obsoleta* and *Hudsonema amabilis* were found in tunnels bored into sodden wood; the former discarded their twig case before entering the wood whereas the latter occurred inside a larval case in the wood.

There are several examples of parallel behaviour between New Zealand and northern hemisphere caddis larvae in exploitation of wood substrates. The wood cases of oeconesids are similar to those of the northern hemisphere Limnephilidae and Lepidostomatidae, and the hollow twig cases of *Triplectides obsoleta* are identical to those of *Heteroplectron californicum* (Calamoceratidae). *T. obsoleta* and *Pycnocentria sylvestris*, have been reported as wood feeders (Rowley-Smith 1962; Cowley 1978) and this was confirmed by gut analysis in the present study; their gouging behaviour is analogous to that of some limnephilids and of *Heteroplectron*. The small size and low density of *P. sylvestris* would probably result in minimal impact on wood debris compared with *T. obsoleta*.

Larvae of *Olinga feredayi* were the most common caddisflies collected on wood substrates. They are scraper-collectors that apparently use the organic film as their primary food source. Gut contents were mostly amorphous detritus with occasional fragments of wood. Their feeding may have some effect on wood degradation, through removal of superficial layers and by exposing new surfaces to microbial attack. Under laboratory conditions, faecal production was relatively high (Table 1) suggesting that they were ingesting a significant amount of wood, but little or no growth was achieved in 4-5 weeks. In the field, both *O. feredayi* and *T. obsoleta* were collected from willow and alder as well as from native woods.

Triplectides obsoleta was the only caddisfly collected that could be considered an important xylophage. The case-making behaviour, feeding habits and method of tunnelling into sodden wood for pupation were described by Rowley-Smith (1962) who stated that "...the distribution of this species will be largely governed by the presence or absence of woody substrates, in order to meet these special requirements of the various stages of the life history." Faecal production of 44% of body weight per day (Table 1) provides some indication of potential feeding impact of *T. obsoleta* larvae.

Table 1. Faecal production rate of wood-associated insects at 15-16°C with wood debris as the only food source. Data expressed as dry wt.

Taxon	No. of larvae	Mean Wt. (mg)	Days	Faecal Production Rate (% of body wt. per day)
<i>Olinga feredayi</i> (Trich.: Conoesucidae)	4	2.63	35	36
	9	1.53	10	28
	10	0.27	28	67
<i>Triplectides obsoleta</i> (Trich.: Leptoceridae)	15	4.50	20	44
<i>Limonia nigrescens</i> (Dipt.: Tipulidae)	12	1.00	28	103
	10	0.88	14	138

Triplectides obsoleta was found in many sites on both islands and was abundant in the low-gradient Styx River, near Christchurch, amongst debris of wood and leaves. Hudson's (1904) comments on this species provide an interesting comparison with the present. He reported that it occurred throughout the country up to 3600 feet, and that it was generally distributed wherever there were dense forests and swift running streams. Its food is "fallen leaves and sodden wood, both of which are present in great quantities in all forest streams." This recorded abundance of wood is in marked contrast to my observations in 1979.

DIPTERA.

Flies were the most abundant and diverse insects associated with wood debris. Taxonomic difficulties precluded definitive identifications of larvae in many families. Amongst the fully aquatic families, larvae of Simuliidae, Dixidae, Blephariceridae, Psychodidae, and Ceratopogonidae use wood as habitat or as attachment sites, but all of these were more common on rock substrates than on wood. Occasional larvae of Dolichopodidae and Empididae (genus *Hemerodromia*, det. H.J. Teskey) were also collected. Pupae and pupal exuviae of *Australosymmerus nitidus* (Family Mycetophilidae, det. P.M. Johns) occurred in wet wood at four sites. Larvae of these large fungus gnats are presumably inhabitants of semi-aquatic areas. Larvae of another family of fungus gnats, Sciaridae, also were collected occasionally from sodden wood which probably came from stream banks rather than in the water.

Two larvae of the family Tanyderidae were collected; one was on the wood surface and the other had bored into a stick. *Mischoderus*, the only genus in New Zealand, is uncommon but widely distributed in stony and soft-bottomed streams (Winterbourn and Gregson 1981). The incidence of a larva in decayed wood may indicate a similar habitat to that of the Australian genus

Eutanyderus which "bore in the surface layers of submerged rotting logs in alpine streams" (Colless and McAlpine 1970).

Larvae of two species of xylophagous chironomids were discovered: *Harrisius pallidus* (Tribe Chironomini) and a member of an undescribed genus in the subfamily Orthoclaadiinae. Both species were widely distributed in the South and North Islands and larvae sometimes occurred in the same stick. *Harrisius* was more abundant, being collected at 12 sites, compared with six sites for the orthoclad species. The larvae tunnelled in superficial layers of soft, fungal-stained branch wood. Because of their small size and concealed habitat they were only found by dissecting the wood under a microscope. *H. pallidus* larvae were first associated with the adult from material collected in water-logged beech at Middle Bush. A larva from this series is keyed and figured by Stark (1981).

Harrisius larvae are pinkish-red with a characteristic flattened thorax and a body form similar to that of North American xylophages in the genus *Stenochironomus*. They occurred within 2-4 mm of the surface, curved in a C-shaped chamber with the ventral side of the body towards the wood surface. Feeding behaviour apparently is similar to that of *Stenochironomus* larvae which press the dorsal and ventral surfaces of the thorax against the wood; if the substrate is too soft they cannot feed (A. Borkent, personal communication, 1980). *Harrisius* larvae removed from their burrows could not bore into soft wood but a few successful transfers were accomplished by placing larvae in cracks in which they then had enough purchase to bore under the surface.

Larvae of the orthoclad species occurred in the same micro-habitat as *Harrisius*. They are white or grey and have a curious horseshoe-shaped plate at the posterior end of the abdomen. Their tunnels were more evident than those of *Harrisius*. The larvae were relatively active when placed on a wood surface but exhibited no swimming ability in water.

Surface-associated chironomid larvae were ubiquitous but none was demonstrated to ingest wood. This is based on gwt analysis of 25 larvae of *Maoridiamesa*, *Polypedilum*, *Paucispinigera*, *Chironomus* and three or four genera of Orthoclaadiinae. However, further study would probably indicate that some species are closely associated with wood debris and utilize it preferentially either as habitat or as a feeding surface. For example, *Chironomus* larvae collected from very decayed logs were observed to build tubes from the wood fines, and several adults (mostly Orthoclaadiinae) emerged from stream wood held in containers in the laboratory.

The Tipulidae, or crane flies, were the most important family of wood degraders encountered during the study. For this family especially, it was useful to adopt a broad interpretation of the aquatic environment as most, if not all, taxa were only semi-aquatic. The occurrence of larvae in sodden wood, whether it is submerged or on the stream bank, results in wood degradation and consequent input of fine particulate material to the stream

system. Because of their relatively large size, they ingest large quantities of wood and egest copious amounts of faecal material. Larvae of the following genera, identified by P.M. Johns, and listed in decreasing order of the number of collection records, were found in rotting wood in close association with small woodland streams: *Limonia*, *Austrolimnophila*, *Leptotarsus*, *Zelandotipula*, *Gynoplistia* (?), *Nothophila*, and *Molophilus* (?).

Limonia nigrescens, the most common tipulid encountered is similar in behaviour and morphology to the *Lipsothrix* spp. studied by Dudley (1982) in Oregon. *L. nigrescens* was collected from several sites in the North and South Islands and a large series of adults emerged in the laboratory. The life cycles of populations at the Kaituna River and Middle Bush Stream were asynchronous. Most larval instars occurred together in some pieces of wood and adults emerge from wood kept in the laboratory throughout the year.

Larval density of *Limonia nigrescens* was relatively high in sodden wood above and below the waterline. Ten to 50 larvae were collected from 50 cm pieces of branch wood of ca 5 cm dia. The larvae occur in tunnels oriented roughly parallel to the surface of the wood. Piles of frass are deposited on the wood surface at the end of the burrow. This material was washed off and weighed to estimate the amount of wood processed (Table 1). Larvae removed from their burrows were successfully transferred to other pieces of decayed wood. Feeding activity of *L. nigrescens* has both a direct and indirect effect on wood degradation. As well as producing frass, some wood is pulped, or macerated, possibly as a result of microbial activity associated with the presence of larvae. Irrespective of the cause of this maceration the net result is a decrease in structural integrity. The softened wood is abraded when exposed to increases in water level or current velocity.

At the end of the growth period, *Limonia nigrescens* larvae bore back to the surface to prepare for pupation. The pupal chamber is curved, with a distinct turret, apparently constructed by the larva digging a small "moat" around the exit hole. Pupation occurs in the chamber below the wood surface. For emergence, the pupa wriggles about half way out of the burrow and the exuviae is left partially exposed when the adult flies away. It is likely that all emergence occurs above the water line.

COLEOPTERA.

Beetles collected from aquatic wood debris included Helodidae larvae, Ptilodactilidae larvae, Elmidae larvae and adults, Hydrophilidae larvae, pupae and adults, Hydraenidae adults, Staphlinidae adults and Cerambycidae larvae. None was abundant, although the helodids and ptilodactilids occurred consistently enough to suggest regular utilization as habitat. Cerambycid larvae are terrestrial wood borers but they were often collected in wet wood and sometimes in submerged pieces. The latter probably indicated recent entry of wood into the water.

The helodid larvae designated as Species A and B by Winterbourn (1978) were tentatively identified as belonging to the genera *Cyphon* and *Metacyphon* by P.M. Johns. They were widespread in occurrence, and were most common in small, forested streams. In a laboratory culture with damp wood as the substrate, nine of 12 larvae survived for 10 weeks. Some scraping was evident on the wood surface, several individuals moulted, and a small amount of faeces was produced but the overall impact on the substrate was minimal. Gut contents of 10 field-collected larvae were primarily detritus, with fungal hyphae being noted occasionally; no wood fragments were observed.

OTHER TAXA.

Two predaceous insects, the semi-aquatic neuropteran, *Kempynus* (Osmylidae) and the megalopteran, *Archichauliodes diversus*, were collected frequently from wood debris. The prosobranch snail, *Potamopyrgus antipodarum* also was common on wood in many areas. Its rasping mode of feeding may scrape some soft material from surface layers. Isopods (Scyphidae) and annelid worms (*Lumbriculus variegatus* and *Eiseniella tetraedra*, det. J. Marshall) were general detritivores found in very rotten wood in aquatic and semi-aquatic habitats. Feeding activities and burrowing by worms would hasten decomposition and worms may well be an important component of the biota during the final stages of wood decay.

COMPARISON OF WOOD-ASSOCIATED INVERTEBRATES IN NEW ZEALAND AND OREGON STREAMS

Winterbourn et al. (1981) stressed the instability and unpredictability of New Zealand streams and noted the relative paucity of wood debris even in forest stream beds. In the present survey, considerably less wood control of channel morphology was observed in New Zealand than in Oregon streams. The conversion of forest lands to agriculture east of the Southern Alps means that there are now few low-gradient streams in areas of native forest. Thus, the perceived lack of wood debris in these streams may well be a relatively recent development. While the role of wood in streams appeared to be limited, both as habitat and as a food base for invertebrates, this may be an artifact of the sites sampled.

Wood is used by the New Zealand fauna in similar ways to that found in Oregon but the impact of the semi-aquatic species seems to be relatively more important than that of fully aquatic insects in New Zealand. Tipulids are the dominant wood processors of saturated wood; *Limonia nigrescens* has a very similar niche to that of *Lipsothrix* spp. in Oregon.

Most of the dominant xylophilous taxa identified in Oregon by Anderson et al. (1978) have functional analogues amongst the New Zealand fauna. *Harrisius pallidus* and an unidentified genus of orthocladine midge are wood borers similar to *Brillia* and *Stenochironomus*. Amongst the wood-surface scrapers there are

representatives of mayflies, stoneflies, caddisflies and beetles in both faunas. However, no New Zealand mayflies appear to be as closely associated with wood as is the North American genus *Cinygma*. Also, no New Zealand beetles were identified as obligate xylophages comparable to the elmid *Lara avara*. In contrast, amongst the stoneflies, *Austroperla cyrene* appeared to have a greater affinity for wood debris than any North American species. A diverse fauna of caddisflies occurs on wood in both areas but wood-cased taxa are under-represented in New Zealand compared with Oregon. *Triplectides obsoleta* is remarkably similar to the North American calamoceratid *Heteroplectron* despite their phylogenetic differences.

In general there are distinct similarities in the manner in which wood debris is exploited by both faunas. These are related to use as a habitat that provides a relatively stable substrate for attachment, concealment, and as a surface for food gathering. The difference between the wood-associated faunas of New Zealand and Oregon is largely a matter of degree of exploitation rather than kind.

ACKNOWLEDGEMENTS

I am especially grateful to M.J. Winterbourn for assistance and advice in developing this project. He not only provided me with a crash course in identification of New Zealand's aquatic invertebrates but also helped with the field studies. For additional taxonomic assistance at the University of Canterbury I thank Peter Johns, Brent Cowie, John Stark and John Marshall. Don Oliver, H.J. Teskey and Art Borkent, Biosystematics Unit, Ottawa, Canada also identified material for me. Linda Roberts analyzed the gut contents of many larvae.

I thank Professor G. Knox for his assistance in arranging for a sabbatical leave at the University of Canterbury and Professor W.C. Clark for providing facilities and support in the Zoology Department.

This project was supported by a National Science Foundation grant DEB 78-10594. An Erskine Grant from the University of Canterbury was especially helpful in deferring travel costs.

This is Technical Paper No. 6368 of the Oregon Agricultural Experiment Station.

LITERATURE CITED

- ANDERSON, N.H. and J.R. SEDELL. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* 24: 351-77.
- ANDERSON, N.H., J.R. SEDELL, L.M. ROBERTS, and F.J. TRISKA. 1978. The role of aquatic invertebrates in processing wood debris in coniferous forest streams. *American Midland Naturalist* 100: 64-82.

- COLLESS, D.H. and D.K. McALPINE. 1970. Diptera. Chapter 34, pp.656-740. In D.F. Waterhouse et al. *The Insects of Australia*. C.S.I.R.O. Melbourne University Press. 1029 pp.
- COWLEY, D.R. 1978. Studies on the larvae of New Zealand Trichoptera. *New Zealand Journal of Zoology* 5: 639-750.
- DUDLEY, T.L. 1982. Population and production ecology of *Lipsothrix* spp. (Diptera: Tipulidae). Unpublished M.S. thesis, Oregon State University, Corvallis. 140 pp.
- DUDLEY, T.L. and N.H. ANDERSON. 1982. A survey of invertebrates associated with wood debris in aquatic habitats. *Melandieria* 39: 1-21.
- HUDSON, G.V. 1904. *New Zealand Neuroptera*. West, Newman and Co., London. 102 pp.
- ROWLEY-SMITH, D.M. 1962. *Studies on the biology and functional morphology of Triplectides obsoleta*. Unpublished M.Sc. Thesis, Zoology Department, University of Canterbury. 142 pp.
- STARK, J.D. 1981. Chironomidae (non-biting midges). In Winterbourn, M.J. and Gregson, K.L.D. *Guide to the aquatic insects of New Zealand*. Bulletin of the Entomological Society of New Zealand. 5: 60-67.
- THIENEMANN, A. 1912. Der Bergbach des Sauerland. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 4: Supp., pp.1-125.
- TOWNS, D.R. 1981. Life histories of benthic invertebrates in a kauri forest stream in northern New Zealand. *Australian Journal of Marine and Freshwater Research* 32: 191-211.
- TRISKA, F.J. and K. CROMACK. 1980. The role of wood debris in forests and streams. In Waring, R.H. (ed.) *Forests: fresh perspectives from ecosystem analysis*. Proceedings of the 40th Biology Colloquium (1979). Oregon State University Press, Corvallis. pp.171-190.
- WINTERBOURN, M.J. 1977. *Biology of the stream fauna*. Chapter 19. In Burrows, C.J. (ed.) *History and Science in the Cass District, Canterbury, New Zealand*: 279-290. University of Canterbury, Christchurch.
- WINTERBOURN, M.J. 1978. The macroinvertebrate fauna of a New Zealand forest stream. *New Zealand Journal of Zoology* 5: 157-169.
- WINTERBOURN, M.J. and K.L.D. GREGSON. *Guide to the aquatic insects of New Zealand*. Bulletin of the Entomological Society of New Zealand. No.5, 80 pp.
- WINTERBOURN, M.J., J.S. ROUNICK, and B. COWIE. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15: 321-328.

APPENDIX

Collecting localities shown in Fig. 1. Numbers in parentheses indicate the number of individual sites visited.

NORTH ISLAND

1. Waitakere River (3)
2. Rotorua (4)
3. Te Wairoa, Tarawera (3)
4. Waitomo (1)
5. Mt. Egmont (2)
6. Tararua Ranges, Levin (3)
7. Upper Hutt (2)
8. Upper Hutt - Paraparaumu Road (2)

SOUTH ISLAND

9. Kaikoura (4)
10. Hundalee (2)
11. Mt. Isobel, Hanmer (6)
12. South Branch, Styx River and tributaries of Avon River, Christchurch (4)
13. Banks Peninsula (5)
14. Geraldine (1)
15. Cave (2)
16. Otematata (1)
17. Tarras (1)
18. Queenstown (3)
19. Arrowtown (1)
20. Haast Pass (1)
21. Mohroe's Creek, Lake Moeraki (2)
22. Craigieburn (1)
23. Cass (2)
24. Arthur's Pass - Otira (2)
25. Lake Brunner area (3)
26. Greymouth - Dobson (4)
27. Punakaiki (1)
28. Charleston (1)
29. Western end of Heaphy Track (4)