

THE BREAKDOWN OF PICEA MARIANA (Mill.) BSP. (BLACK SPRUCE) NEEDLES
IN A RECENTLY CREATED NORTHERN RESERVOIR,
SOUTHERN INDIAN LAKE, MANITOBA

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BY

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IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY



MAY 1986

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A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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ABSTRACT

Formation of the Southern Indian Lake reservoir, northern Manitoba, added an estimated 5.4×10^5 tonnes of Picea mariana (black spruce) needles to the lake. The breakdown and macroinvertebrate colonization of needles in the lake was followed by stringing needles on monofilament line, placing the strings into 3 mm-mesh bags, and situating the bags along four shorelines representing different shoreline types (clay vs bedrock) and wave exposures (highly exposed vs protected). Sampling was done in 0-41 d and 328-384 d phases. Effects of excluding macroinvertebrates were tested by using needle strings placed in 50 μm -mesh bags at the clay low exposure shoreline.

Needle breakdown occurred in two stages. Initial weight losses were primarily due to leaching and microbial conditioning. Subsequent weight losses were primarily due to macroinvertebrate feeding and/or wave action. Over the entire 384 d period, leaching and microbial conditioning each accounted for $\approx 30\%$ of total weight losses. Macroinvertebrates accounted for $\approx 40\%$ of total weight losses. High wave energies increased weight losses by as much as 18%, while heavy sediment deposition decreased weight losses by up to 30%. Processing coefficients (k) for the entire 384 d ranged from 0.0011 d^{-1} for the 50 μm -mesh packs to 0.0097 d^{-1} for the 3 mm-mesh packs at the bedrock high exposure shoreline.

Macroinvertebrate colonization of needle strings occurred rapidly ($>3 \text{ d}$) and was mainly by chironomid larvae. Colonization was due to macroinvertebrates present both within the surrounding bottom substrate

and drifting within the water column. Most chironomid larvae colonized the surface of the needles, however, Phaenopsectra punctipes (Wied.) and Brillia flavifrons (Joh.) larvae appeared to mine into the mesophyll region of the needles and consume them from inside. Heavy wave action, heavy sediment deposition, and the reduction of needle surface area as breakdown proceeded reduced the numbers of colonizing macroinvertebrates and caused large shifts in the structure of colonizing chironomid communities. P. punctipes was the dominant colonizer at all shorelines except those with heavy sediment deposition. At such shorelines, Microtendipes and Procladius were dominant.

Values of k for Southern Indian Lake most resemble those for conifer needle breakdown in streams, indicating the significance of wave action in the lake. The breakdown of P. mariana needles in Southern Indian Lake appeared to be a significant source of carbon during the year following impoundment, and needles may have been an important habitat for macroinvertebrates within localized areas.

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CHAPTER ONE

GENERAL INTRODUCTION

The breakdown of terrestrial vegetation in aquatic habitats can release large amounts of energy (organic C) to the biotic communities of streams (e.g. Nelson and Scott 1962; Minshall 1967; Fisher and Likens 1972, 1973; Hynes 1975; Iversen et al. 1982), rivers (e.g. Mathews and Kowalczewski 1969), ponds (e.g. Hodgkinson 1975b; Bärlocher et al. 1978b), and lakes (e.g. McConnell 1968; Pieczynska 1972; Hall and Hyatt 1974; Aioi and Yamamoto 1976; Gasith and Hasler 1976; Rau 1976, 1980; Wissmar et al. 1977). Large amounts of terrestrial vegetation are often inundated during the formation of new reservoirs. Breakdown of this vegetation represents a potentially important source of energy to the biotic community during the initial years following reservoir formation.

The impoundment of Southern Indian Lake, in northern Manitoba, inundated $\approx 1.2 \times 10^7$ tonnes of terrestrial vegetation (G.K. McCullough, Freshwater Institute, Winnipeg, Manitoba, pers. comm.). Much of this vegetation was tree bole, which is highly resistant to breakdown (Anderson et al. 1978), but large quantities of Picea mariana (Mill.) BSP. (black spruce) needles were also added to the lake as a result of the flooding. These needles may be important to the biotic community of the reservoir, either through the release of energy during breakdown or through the creation of favorable habitats for colonization by aquatic macroinvertebrates (McLachlan 1970, 1974; Cherry and Guthrie 1975; Baxter 1977).

Compared to deciduous leaves, little information exists on the breakdown of conifer needles in streams (e.g. Sedell et al. 1975; Triska et al. 1975; Bärlocher et al. 1978a; Triska and Buckley 1978; Short et al. 1980; Rossett et al. 1982), and even less information exists on conifer needle breakdown in ponds and lakes (e.g. Hodgkinson 1975a; Rau 1978; Tiwari and Mishra 1983). No information is available on the breakdown on conifer needles in new reservoirs, and little is known about the breakdown of either deciduous leaves or conifer needles in northern waters.

The objectives of this study were as follows: (1) to examine the processes and factors influencing the breakdown of P. mariana needles in a new northern reservoir, Southern Indian Lake; (2) to examine the colonization of P. mariana needles in Southern Indian Lake by aquatic macroinvertebrates; (3) to examine the release of energy (organic C) to the biotic community of Southern Indian Lake by the breakdown of inundated P. mariana needles during the initial years following impoundment; and (4) to compare and contrast the breakdown of P. mariana needles in Southern Indian Lake with the breakdown of leaf and needle species in other aquatic habitats.

CHAPTER TWO

STUDY SITE

Southern Indian Lake (lat. 57°N, long. 99°W) is a major lake on the Churchill River in north-central Manitoba (Fig. 1), and lies on the western arm of the Precambrian Shield. The geology of the region is dominated by intrusive granitic rocks with extensive areas of gneissic and volcanic rocks [Frohlinger 1972; Lake Winnipeg, Churchill and Nelson Rivers Study Board (= LWCNRSB) 1975]. The bedrock surface was heavily glaciated during the Pleistocene epoch and was formed into a plain with low rounded hills (<50 m) and shallow valleys (Newbury et al. 1978). Surficial deposits of glacial, glacio-fluvial, and glacio-lacustrine origin overlie the bedrock in thicknesses varying from 0-5 m in elevated areas and up to 30 m in valleys (Newbury et al. 1978). Fine-grained varved clays, deposited in glacial Lake Agassiz during the late Pleistocene, dominate surficial deposits throughout the south-eastern two-thirds of the lake basin (Newbury et al. 1978). A well-developed organic layer, usually >0.3 m in thickness, overlies most deposits (Newbury et al. 1978).

Discontinuous permafrost is widespread throughout the Southern Indian Lake region (Brown and Pewe 1973). The average depth to permafrost conditions is 63 cm (Newbury et al. 1978). Regular ice banding, each band a few millimeters in thickness, occurs in all fine-grained surficial deposits, with occasional ice lenses up to 8 cm in thickness (Newbury et al. 1978).

Boreal forest, interspersed with extensive areas of muskeg, surrounds the lake (LWCNRSB 1975; Newbury et al. 1978). Picea mariana (Mill.) BSP. (black spruce) is the dominant tree species (LWCNRSB 1975). Sporadic stands of Picea glauca (Moench) Voss (white spruce) and Pinus banksiana Lamb. (jack pine) occur in well-drained areas such as flood plains, eskers, and bedrock outcrops (LWCNRSB 1975). Populus tremuloides Michx. (trembling aspen), Populus balsamifera L. (balsam poplar), Betula papyrifera Marsh. (white birch), Salix spp. (willow), and Alnus spp. (alder) are common in near-shore areas (LWCNRSB 1975; Newbury et al. 1978). Sphagnum spp. (sphagnum moss), Pleurozium schreberi (Brid.) Mitt. (feather moss), Hylocomium splendens (Hedw.) BSG (feather moss), Cladonia spp. (lichen), and Ledum groenlandicum Oeder (Labrador tea) form most of the ground cover (LWCNRSB 1975; Newbury et al. 1978).

Southern Indian Lake lies in the subarctic climate zone (Newbury et al. 1984). Mean monthly air temperatures vary between -25°C in January and +15°C in July with a mean annual temperature of -4°C (Newbury et al. 1984). The frost-free period each year is ≈ 80 d in length (LWCNRSB 1975). The average ice-free season extends from mid May to late November (Newbury et al. 1984). Mean annual precipitation is ≈ 525 mm (McCullough 1981) of which nearly two-thirds falls as rain during the summer months (LWCNRSB 1975).

In 1977, $\approx 85\%$ ($850 \text{ m}^3 \text{ s}^{-1}$) of the flow of the Churchill River through Southern Indian Lake was diverted across the drainage divide

separating the Churchill and Nelson River basins. Diversion was accomplished by damming the natural lake outlet at Missi Falls (summer 1976), causing the water to rise 3 m above long-term lake levels of 255 m MSL (McCullough 1981), and allowing water to flow by gravity through a previously constructed diversion channel (Fig. 1; LWCNRSB 1975; Newbury et al. 1984). Once in the Nelson River basin, the diverted waters flow through 300 km of tributary valleys to the main Nelson River channel, supplying additional water flow to a 30 yr, 10,000 MW hydroelectric scheme currently being developed (LWCNRSB 1975; Newbury et al. 1984).

The impoundment of Southern Indian Lake flooded $\approx 346 \text{ km}^2$ of surrounding terrestrial area, increasing the surface area of the lake to 2391 km^2 (McCullough 1981). Mean water depth increased $\approx 1.3 \text{ m}$ to 9.8 m and water residence time increased from 190 d to 263 d (McCullough 1981). Over three-quarters of the length of flooded shoreline is fine-grained frozen silts and clays, subject to permafrost melting, solifluction, and wave erosion (Newbury et al. 1978; Newbury and McCullough 1984). Rates of erosion, for silt and clay shorelines, vary from $<1 \text{ m}^3$ to $>23 \text{ m}^3$ per m of shoreline during the open-water season, depending upon the exposure of the shoreline to wave action and the composition of the backshore materials (Newbury et al. 1978; Newbury and McCullough 1984). Approximately 80% of the eroded material is deposited within 200 m of shore (Hecky and McCullough 1984). The minimum period before $\approx 80\%$ of the shoreline surrounding Southern Indian Lake becomes restabilized is estimated to be 35 yr (Newbury and McCullough 1984).

CHAPTER THREE

THE BREAKDOWN OF PICEA MARIANA NEEDLES IN SOUTHERN INDIAN LAKE

INTRODUCTION

Leaf breakdown in freshwaters is the conversion of whole leaves to large particulate organic matter (LPOM, particle size $>1 <4$ mm), fine particulate organic matter (FPOM, particle size $>0.005 <1$ mm), dissolved organic matter (DOM, particle size <0.005 mm), animal and microbial biomass, and CO_2 (Cummins 1974; Petersen and Cummins 1974; Boling et al. 1975; Cummins et al. 1980). This conversion depends upon a number of interacting processes, including the leaching of water soluble substances, microbial conditioning, and macroinvertebrate feeding (Petersen and Cummins 1974; Boling et al. 1975; Barnes et al. 1978; Webster and Simmons 1978; Anderson and Sedell 1979; Hanlon 1982).

Terrestrial leaves entering lotic systems usually lodge in packs on the upstream side of obstructions (e.g. cobbles, boulders, or wood debris) or settle in areas of reduced current (e.g. pools or eddies behind large obstructions) (Anderson and Sedell 1979). Leaves entering lentic systems usually float for several days before sinking and accumulating in the littoral zone (Aioi and Yamamoto 1976; Gasith and Hasler 1976). In the littoral zone, the leaves tend to become either uniformly distributed or aggregated around obstructions and may be on top of, or buried within, the sediments (Gasith and Lawacz 1976).

Immediately upon wetting, leaves begin to lose 5-40% of their initial biomass through the leaching of water-soluble substances

(Petersen and Cummins 1974; Saunders 1975). Carbohydrates, polyphenols, amino acids, terpenes, and non-volatile aliphatic acids are common leachates (Suberkropp et al. 1976; Peters et al. 1976; Blaschke 1979). Leaching is essentially complete within 24 h for most deciduous leaves (Nykvist 1959a, 1961a; Petersen and Cummins 1974; Saunders 1975). However, the leaching of conifer needles may continue for up to 20 d (Nykvist 1959b, 1961b), possibly due to the presence of impermeable waxes within the needle cuticle (Millar 1974).

Under aerobic conditions, most leachates are either rapidly metabolized by microorganisms or are flocculated by a combination of abiotic and microbial factors to form FPOM (Lush and Hynes 1974). Other leachates, notably tannins and terpenes, are not easily metabolized and can inhibit microbial and macroinvertebrate growth and leaf breakdown processes (Peters et al. 1976; Cameron and LaPoint 1978; Blaschke 1979; Andrews et al. 1980). As a result, leaching must be complete before the breakdown of leaf species containing these inhibitor compounds can proceed any further.

Once leaching has been completed, microorganisms begin to colonize the leaf material. Fungi, especially aquatic hyphomycetes, appear to be the dominant colonizers (Kaushik and Hynes 1968, 1971; Bärlocher and Kendrick 1974; Suberkropp and Klug 1974, 1976; Summerbell and Cannings 1981). Bacteria may also be important, especially under anaerobic conditions or on leaf fragments too small for fungi to colonize (Saunders 1975).

Microbial colonization appears necessary to condition the leaves in preparation for macroinvertebrate colonization and feeding. Most aquatic macroinvertebrates have difficulty digesting leaf structural compounds such as cellulose and lignin (Bjarnov 1972; Berrie 1975; Monk 1976). However, the colonizing microorganisms produce enzymes capable of breaking these compounds into subunits easily digested by macroinvertebrates (Bärlocher and Kendrick 1975; Suberkropp and Klug 1980). The breakdown of cellulose and lignin also softens the leaf material allowing easier ingestion by macroinvertebrates (Suberkropp and Klug 1980).

Once leaf material has been microbially conditioned, further breakdown depends mainly upon the feeding activities of aquatic macroinvertebrates (Cummins 1973; Cummins and Klug 1979). Whole leaves and LPOM are fed upon by macroinvertebrate detritivores known as shredders (Boling et al. 1975). Typical shredders are found within the Plecoptera (Filipalpia), Trichoptera (Limnephilidae and Lepidostomatidae), and Diptera (Tipulidae and Chironomidae) (Cummins 1973; Merritt and Cummins 1978). Their mode of feeding involves biting and chewing leaf material, and results in a reduction of particle size. They are able to assimilate $\approx 40\%$ of what they ingest (Welch 1968; Berrie 1975). The remainder is egested as feces which enter the FPOM pool and are subject to further microbial conditioning and subsequent macroinvertebrate feeding (Boling et al. 1975). Cummins (1974) found that shredder feeding also helps to increase the microbial conditioning of leaves by exposing new surfaces for microorganisms to colonize.

FPOM, including leaf fragments and shredder feces, is predominantly fed upon by macroinvertebrates known as collectors (Boling et al. 1975). Typical collectors are found within the Ephemeroptera (Siphonuridae and Baetidae), Trichoptera (Philopotamidae and Hydropsychidae), and Diptera (Simuliidae and Chironomidae) (Cummins 1973; Merritt and Cummins 1978). Their principle modes of feeding are gathering, sweeping, and filtering. Little or no chewing is involved. Welch (1968) found that collectors were able to assimilate 25-30% of what they ingested and, as with shredders, the remainder was egested as feces which re-enter the FPOM pool (Boling et al. 1975). Collector feeding can increase or decrease particle size within the FPOM pool but usually the feces are similar in size to the ingested particles (Cummins 1973; Boling et al. 1975; Cummins and Klug 1979). FPOM continues to cycle (e.g. ingestion-partial assimilation-egestion) through the collector community until breakdown is complete and all organic matter has been converted to microbial biomass, animal biomass, and CO₂ (Cummins 1973; Petersen and Cummins 1974).

In lotic systems, FPOM does not cycle in place but is displaced downstream each time the cycle (see above) is completed (Webster and Patten 1979). As a result, the collector communities of lotic systems are dependent upon FPOM that has been cycled by upstream communities (Cummins 1980). This coupling of downstream transport and FPOM cycling is known as spiralling and is embodied in the "Nutrient Spiralling Concept" proposed by Webster (1975). The efficiency of FPOM spiralling

is determined by the downstream distance required to complete one loop of the spiral (spiralling length) (Newbold et al. 1981). The shorter the spiralling length the more efficiently FPOM is cycled within the system.

FPOM spiralling does not occur in lentic systems as there is no unidirectional flow of water. Instead, wave action tends to transport FPOM to offshore areas where it is deposited in the profundal sediments (Komar 1976; Baxter 1977; Goldman and Kimmel 1978; Dudgeon 1982). The deposited FPOM is then cycled by the feeding and bioturbation activities of sediment-feeding collectors (gatherers) (Davis 1974; McLachlan and McLachlan 1976; Gallepp et al. 1978; Gallepp 1979; Graneli 1979a, b). The efficiency of FPOM cycling in lentic systems is represented by the rate at which incompletely broken down FPOM accumulates within the deeper areas of the system (Goldman and Kimmel 1978). Accumulation occurs most rapidly in systems where the efficiency of FPOM cycling is low.

Many factors can influence the processes involved in leaf breakdown, resulting in differences in breakdown rate between systems or between sites within the same system. These factors include the presence or absence of macroinvertebrates (Petersen and Cummins 1974; Iversen 1975; Sedell et al. 1975; Webster and Simmons 1978); the leaf or needle species involved (Kaushik and Hynes 1971; Petersen and Cummins 1974; Hart and Howmiller 1975; Webster and Simmons 1978; Herbst 1982); water temperature (Petersen and Cummins 1974; Iversen 1975; Suberkropp

et al. 1975); dissolved nutrient concentration of the water (Kaushik and Hynes 1971; Howarth and Fisher 1976; Triska and Buckley 1978; Elwood et al. 1981); substrate particle size distribution (Reice 1974); stream current velocity (Reice 1977; Meyer 1980; Pidgeon and Cairns 1981; Webster and Waide 1982); sedimentation rate (Herbst 1980; Meyer 1980; Webster and Waide 1982); and water depth (Barnes et al. 1978; Webster and Simmons 1978; Reed 1979; Tiwari and Mishra 1983).

Analogues of natural leaf accumulations have been extensively used to study leaf breakdown in both terrestrial and aquatic ecosystems since the method was first employed in woodland systems by Bocock and Gilbert (1957). These analogues are designed to: (1) place a known amount of leaf material into a selected position within the study system; (2) keep the leaf material exposed to the natural and/or experimental conditions present; and (3) allow retrieval of the partially broken-down leaf material and the associated microbial and macroinvertebrate colonizers after a predetermined length of time. In aquatic systems, litter bags, consisting of whole leaves (e.g. Mathews and Kowalczewski 1969; Hart and Howmiller 1975; Hodgkinson 1975a; Gasith and Lawacz 1976; Cameron and LaPoint 1978; Webster and Simmons 1978; Meyer 1980; Pidgeon and Cairns 1981; Hanlon 1982; Webster and Waide 1982) or discs cut from leaf material (e.g. Kaushik and Hynes 1971; Iversen 1973, 1975; Bärlocher and Kendrick 1975) enclosed within bags of various mesh sizes, have been used extensively. Leaf packs, consisting of leaves tethered, strung, or loosely bound together, have also been used extensively (e.g. Petersen

and Cummins 1974; Reice 1974, 1977; Sedell et al. 1975; Triska et al. 1975; Barnes et al. 1978; Rau 1978; Herbst 1980; Short et al. 1980).

The objectives of this chapter were as follows: (1) to examine the influence of shoreline type (clay vs bedrock) and wave exposure (low vs high) on the breakdown of P. mariana needles in Southern Indian Lake and (2) to determine the roles played by leaching, microbial conditioning, and macroinvertebrate activity in this breakdown.

MATERIALS AND METHODS

Needle pack construction and installation

Needle packs, each consisting of a string of needles enclosed within a nylon mesh bag, were used in this experiment. Needles were removed from freshly cut P. mariana branches and strung on a 6 lb test monofilament fishing line to produce 1-2 g needle strings. Each string was oven-dried at 100°C for 24 h, weighed, placed into a 3 mm hexagonal mesh nylon bag (10 x 10 cm) and the bag was sewn closed (Fig. 2).

Needle packs were attached along 3 m lengths of vinyl-covered galvanized clothesline wire and anchored, using SCUBA (Self-Contained Underwater Breathing Apparatus), in 2 m of water, parallel to each of four shorelines. These shorelines were chosen to represent high and low erosion rates and exposures to wave energy (Table 1). The shorelines did not differ with respect to O₂ concentration, conductivity, or temperature over the duration of the study.

To examine the influence of macroinvertebrates on needle breakdown rates, needle strings were enclosed within 50 µm-mesh nylon bags (Fig.

2), to exclude macroinvertebrates, and were anchored at the clay low exposure shoreline. This shoreline was chosen because colonization of stick-chain artificial substrates indicated that it was likely to provide maximum numbers of macroinvertebrates (D.M. Rosenberg and A.P. Wiens, Freshwater Institute, Winnipeg, Manitoba, unpubl. data). Low wind-wave energies present at this shoreline (Table 1) would also minimize the potential effects of mechanical abrasion within the 50 μ m packs (see Discussion - Needle pack effects).

Sampling and statistical design

Three 3 mm-mesh needle packs from each shoreline and three 50 μ m-mesh packs from the clay low exposure shoreline were removed, using SCUBA, at intervals of 0 (28 July 1979), 3, 5, 13, 20, 27, 34, 41 (7 September 1979), 328 (20 June 1980), 335, 342, 356, 363, 370, 377, and 384 d (15 August 1980). Needle packs were not removed over the cold-weather period (41-328 d). The lake was covered with ice from approximately day 100 (4 November 1979) to day 300 (24 May 1980) (G.K. McCullough, Freshwater Institute, Winnipeg, Manitoba, pers. comm.).

During removal, each pack was detached from the clothesline wire, immediately enclosed within a plastic bag to prevent the loss of needle fragments and colonizing macroinvertebrates, and brought to the surface. The needle packs were returned to the laboratory where the macroinvertebrates were live-sorted, counted, and preserved in 70% ethanol. Ostracods, copepods, and cladocerans were not enumerated

because they could not be sampled quantitatively. The strings were then gently washed to remove attached debris, oven-dried at 100°C for 24 h, and reweighed. Needle packs installed and removed on day 0 indicated only a 2-3% error in needle string weight losses due to handling. This error was not significant (paired t-test, $p > 0.05$; Snedecor and Cochran 1980) and, therefore, experimental data were not corrected.

Needle string weight losses were expressed as the percentage of initial needle material remaining (% R) at time t. Needle breakdown coefficients (k) were calculated for 0-41 d, 328-384 d, and 0-384 d using the negative exponential model (Jenny et al. 1949; Petersen and Cummins 1974):

$$-k = \frac{\log_e (\% R/100)}{t}$$

This model assumes a constant fractional loss of needle material with time.

The Kleinbaum and Kupper (1978) dummy-variable method was used to compare significant weight loss regressions ($\log_e R$ vs time) as follows: (1) high exposure shorelines to low exposure shorelines; (2) clay shorelines to bedrock shorelines; and (3) 50 μ m-mesh packs to 3 mm-mesh packs at the clay low exposure shoreline. Significance of the weight loss regressions was tested using analysis of variance (ANOVA; Snedecor and Cochran 1980).

Gut content analysis

The gut contents of all chironomid larvae mounted for taxonomic identification (see Chapter Four - Materials and Methods) were examined for the presence of vascular plant tissue as evidence of feeding activity. Aquatic macrophytes did not occur at any of the study shorelines and little terrestrial leaf litter was observed by using SCUBA, so any vascular plant tissue present within the guts of the larvae was assumed to be ingested needle material. Amounts of ingested needle material were not quantified.

RESULTS

Needle string weight losses

Needle strings remained intact with no evidence of fragmentation from 0-41 d. The density of colonizing fungi was observed to increase throughout this 41 d interval. Needle tissue became darkened in areas of intense fungal colonization. Approximately 25% of the initial needle string dry weight was lost in the first 3 d, followed by a further loss of $\approx 6\%$ over the next 38 d (Fig. 3). All weight loss regressions ($\log_e \% R$ vs time) for 0-41 d were significant ($p < 0.01$). Comparisons of regressions for the different shoreline types and wave exposures indicated no significant differences ($p > 0.05$; Kleinbaum and Kupper 1978). Exclusion of macroinvertebrates also had no effect on weight loss during the 0-41 d period ($p > 0.05$). The mean breakdown coefficient for 0-41 d was 0.0055 d^{-1} (Table 2).

Sampling at the end of winter (328 d) revealed that needle strings in the 3 mm-mesh packs were fragmented at all shorelines except the clay high exposure. The mesophyll region of the needles appeared to be especially affected. Needle packs at the clay high exposure shoreline, unlike the other study shorelines, were covered by ≈ 2 cm of sediment, presumably eroded from the shoreline itself. Needle string dry weight remaining in 3 mm-mesh packs at 328 d ranged from 6% of the original at the bedrock high exposure shoreline to 52% at the clay high exposure shoreline (Fig. 3).

By the end of the experiment (384 d), 3% of the initial needle string dry weight remained in 3 mm-mesh packs at the bedrock high exposure shoreline (Fig. 3). Proportions remaining in 3 mm-mesh packs at the clay low exposure, bedrock low exposure, and clay high exposure shorelines were 6%, 19%, and 44%, respectively. Individual weight loss regressions ($\log_e \% R$ vs time) for 328-384 d were significant ($p < 0.05$) only at the clay low exposure shoreline ($k = 0.0329 \text{ d}^{-1}$; Table 2) so comparisons of shoreline types and wave exposure were not done for this period.

No fragmentation of needles was observed in the 50 μm -mesh packs during the 328-384 d period. At 328 d, 58% of the initial needle string dry weight remained in the 50 μm -mesh packs and 51% remained at 384 d (Fig. 3). The breakdown coefficient for 50 μm -mesh packs during 328-384 d was 0.0033 d^{-1} (Table 2). Comparison of weight loss regressions ($\log_e \% R$ vs time) for 3 mm-mesh and 50 μm -mesh packs at the clay low

exposure shoreline indicated that the exclusion of macroinvertebrates significantly reduced weight losses during 328-384 d ($p < 0.01$; Kleinbaum and Kupper 1978).

Breakdown coefficients for the entire study period (0-384 d) ranged from 0.0011 d^{-1} for the 50 μm -mesh packs at the clay low exposure shoreline to 0.0097 d^{-1} for the 3 mm-mesh packs at the bedrock high exposure shoreline (Table 2). The lowest breakdown coefficient for 3 mm-mesh packs was recorded at the clay high exposure shoreline (0.0019 d^{-1}). Intermediate values of 0.0041 and 0.0070 d^{-1} were calculated for 3 mm-mesh packs at the bedrock and clay low exposure shorelines, respectively. Comparisons of shoreline types and wave exposures for the 0-384 d period were significant ($p < 0.01$; Kleinbaum and Kupper 1978). Comparison of weight loss regressions ($\log_e \% R$ vs time) for 3 mm-mesh and 50 μm -mesh packs at the clay low exposure shoreline indicated exclusion of macroinvertebrates significantly ($p < 0.01$) reduced weight losses in the 50 μm -mesh packs during 0-384 d.

Macroinvertebrates

Macroinvertebrate colonization of the 3 mm-mesh packs began within 3 d of installation and continued over the duration of the experiment (384 d; Figs. 4 and 5). Chironomid larvae comprised $>50\%$ of the colonizing macroinvertebrates. Most macroinvertebrates colonized the surface of the needles, but some chironomid larvae [e.g. Brillia flavifrons (Joh.) and Phaenopsectra punctipes (Wied.)] were found within

the mesophyll region of individual needles. Negligible colonization of the 50 μ m-mesh packs (i.e. <3 individuals per string) was observed.

No vascular plant tissue was found in the guts of chironomid larvae colonizing needle packs during 0-41 d. During 328-384 d, 16% of the larvae within 3 mm-mesh packs at the clay low exposure shoreline had ingested needle material (Table 3). Eight percent, 6%, and 1% of the larvae colonizing needle strings at the bedrock low exposure, bedrock high exposure, and clay high exposure shorelines, respectively, had ingested needle material. Fragments of needle material were present in the guts of all chironomid larvae (mostly P. punctipes) found within the mesophyll region of individual needles.

DISCUSSION

Needle pack effects

The needle packs used in this experiment may have influenced the rates of needle breakdown observed. Therefore, it is essential that any potential influence be understood before needle breakdown in Southern Indian Lake is discussed.

Fragments of incompletely broken-down needle material, up to 3 mm in size (LPOM and FPOM), may have been lost from the 3 mm-mesh packs. As a result, weight losses from the 3 mm-mesh packs do not necessarily represent the complete breakdown or conversion of needle material to microbial biomass, animal biomass, and CO₂ (Petersen and Cummins 1974) in Southern Indian Lake. Unfortunately, the amounts of incompletely broken-down needle material lost from the packs are not known.

The puncturing of needles during stringing may have accelerated the leaching of water soluble substances resulting in an overestimate of initial (0-3 d) breakdown. Rau (1978), working with Abies amabilis Doug. ex Forbes (Pacific silver fir) and Tsuga mertensiana (Bong.) Carr. (mountain hemlock) needles in Findley Lake, Washington, found an initial rapid weight loss similar to that in the present experiment [$\approx 23\%$ in 10 d (Rau 1978) cf $\approx 25\%$ in 3 d (Fig. 3)] when strung needles were used but, a slower initial loss occurred when intact needles enclosed in mesh bags were used [8-14% in 10 d (Rau 1978)]. Accelerated leaching should not affect breakdown rates calculated for 0-41 d, 328-384 d, and 0-384 d periods because the leaching of Picea needles is essentially complete by 20 d (Nykvist 1959b, 1961b; Ostrofsky 1978).

Oven-drying of the needle strings prior to submergence (100°C for 24 h) may have influenced rates of needle string breakdown by causing changes in the chemical composition of the needles (N.H. Anderson, Dept. of Entomology, Oregon State University, Corvallis, Oregon, pers. comm.). Although many breakdown studies have used oven-dried leaves (e.g. Mathews and Kowalczewski 1969; Bärlocher and Kendrick 1973; Hart and Howmiller 1975; Hodkinson 1975a; Benfield et al. 1977; Davis and Winterbourn 1977; Reice 1977, 1978; Eidt and Meating 1978; Blackburn and Petr 1979; Herbst 1980, 1982; Short et al. 1980; Short and Ward 1980; Pidgeon and Cairns 1981; Hanlon 1982), the effects of oven-drying are not understood. For example, oven-drying may increase breakdown rates by denaturing and/or solubilizing organic materials such as proteins

(Jenkinson 1966; Spalding 1978) or may decrease breakdown rates by heat-catalyzed browning in which lignin and N-containing compounds (e.g. proteins) form chemical complexes that are highly resistant to breakdown (Suberkropp et al. 1976).

While drying may affect needle breakdown rates it did not appear to affect the initial colonization by macroinvertebrates. Experiments with 3 mm-mesh packs containing strings of either oven-dried or fresh (not dried) needles indicated no significant differences (two-way ANOVA; $p > 0.05$) in the numbers of colonizing macroinvertebrates due to drying of the needles (see Chapter Four - Checks on experimental methods).

Large macroinvertebrate shredders, such as Trichoptera, may have been excluded by the 3 mm-mesh, resulting in an underestimate of natural needle breakdown rates within these packs. However, this may not be a problem because Trichoptera appear to be rare in Southern Indian Lake (Resh et al. 1983). Furthermore, Benfield et al. (1977) found that large macroinvertebrate shredders present in low numbers contributed very little to the breakdown of Plantanus occidentalis L. (American sycamore) leaves placed into the North Fork of the Roanoke River, Virginia.

Breakdown rates within the 50 μ m-mesh packs may have been underestimated, resulting in an overestimate of the effects of excluding macroinvertebrates. The 50 μ m-mesh may have restricted the flow of water through the packs, reducing physical abrasion of needles within the packs (Petersen and Cummins 1974; Rau 1978), and producing anaerobic

conditions which would inhibit microbial breakdown processes (Petersen and Cummins 1974). However, the effects of reduced physical abrasion on needle string weight losses should be minimal because of low wind-wave energies at the clay low exposure shoreline (Table 1; see also Chapter Six - Partitioning of needle pack breakdown). The importance of anaerobic conditions to needle breakdown in the 50 μ m-mesh packs is not known.

It was impossible to separate the macroinvertebrates colonizing needle strings within the 3 mm-mesh packs from those macroinvertebrates colonizing the mesh bags. As a result, macroinvertebrate numbers observed during this experiment (Fig. 4) include macroinvertebrates colonizing both the needle strings and the mesh bags. This is not considered to be a problem, however, because in an experiment comparing the colonization of 3 mm-mesh needle packs and empty 3 mm-mesh bags, the macroinvertebrates selectively colonized the P. mariana needles (see Chapter Four - Checks on experimental methods).

Effects of leaching and microbial conditioning

Neither differences in shoreline type and wave exposure nor the presence of macroinvertebrates appeared to be important to needle breakdown during the initial 41 d of the experiment. Most of the breakdown during the 0-41 d period was simply a function of the packs being immersed in water (cf. Reice 1977).

Leaching and microbial conditioning probably were responsible for needle string weight losses during 0-41 d. The leaching of water

soluble substances occupied the period of initial rapid weight loss ($\approx 25\%$ in 3 d, Fig. 3; see also Petersen and Cummins 1974). Accelerated leaching, by the stringing of needles (see Needle pack effects, above), does not appear to have affected either the total amount of material lost or the breakdown coefficients calculated for the 0-41 d period. Water soluble substances comprise $\approx 25\%$ of the dry weight of Picea needles and these substances leach at a k of $\approx 0.005 \text{ d}^{-1}$ over a 42 d period (from Ostrofsky 1978). These values are similar to ones obtained by the present experiment (Fig. 3; Table 2).

Fungal colonization first occurred within 13 d of the start of the experiment, indicating the beginning of a microbial conditioning period (Suberkropp and Klug 1974; Bärlocher et al. 1978a). Darkening of needle tissue in areas of intense fungal colonization indicated that the chemical nature of the needles was being altered, possibly by enzymatic activity (Summerbell and Cannings 1981). Electron microscopy has shown that microbial conditioning of leaf material may begin within 3 d of submergence in a stream (Cummins 1974).

Effects of macroinvertebrates

Evidence of the importance of macroinvertebrates to needle breakdown in Southern Indian Lake is provided by the following observations:

- (1) Needle tissue was present in the guts of chironomid larvae, particularly P. punctipes, colonizing needle strings during 328-384 d.

The percentages of collected larvae ingesting needle material correlate well with rates of needle breakdown at all shorelines, except for the bedrock high exposure shoreline (i.e. percentage of collected larvae ingesting needle material at clay low exposure > bedrock low exposure > clay high exposure; Table 3, Fig. 3). Macroinvertebrate feeding probably contributed most to needle breakdown at the clay low exposure shoreline and least to needle breakdown at the clay high exposure shoreline where feeding was inhibited by the effects of heavy sediment deposition (see Effects of shoreline type and exposure to waves, below). Physical breakdown processes were more important at the bedrock high exposure shoreline (see Effects of shoreline type and exposure to waves, below), so this shoreline did not fit the ranking.

(2) Higher weight losses and breakdown coefficients occurred in the 3 mm than in the 50 μ m-mesh packs during the 384 d experiment (Fig. 3; Table 2).

(3) Needles in 3 mm-mesh packs were extensively fragmented between day 41, the last sampling date before winter, and day 328, the first sampling date following winter. Fragmentation of the needles probably occurred under ice-cover when wave energies were not being generated, and water temperatures were near 0°C (Hecky et al. 1979). Work in a Washington subalpine lake (Rau 1978) and in a Colorado mountain stream (Short et al. 1980) indicated that macroinvertebrate feeding may be greatest during mid-winter at water temperatures near 0°C.

Differences in the extent of microbial conditioning can be used to explain the proportions of collected chironomid larvae ingesting needle

material during both 0-41 d and 328-384 d periods. Highly conditioned foods appear to be a more preferred food source to aquatic macroinvertebrates and are ingested more often than less conditioned foods (Kaushik and Hynes 1971; Bärlocher and Kendrick 1975; Bärlocher et al. 1978a; Bärlocher and Rossett 1981; Summerbell and Cannings 1981). Needle material was ingested during 328-384 d, but not during 0-41 d, indicating that the needles were not sufficiently conditioned to be palatable to chironomid larvae during 0-41 d. A similar two-stage breakdown of leaching/microbial conditioning followed by macroinvertebrate feeding was reported by Sedell et al. (1975) and Bärlocher et al. (1978a) for the conifer needles used in their studies.

During 328-384 d, the highest percentage of collected chironomid larvae ingesting needle material may have occurred at the clay low exposure shoreline because needles at this shoreline were more highly conditioned compared to needles at the other shorelines. The lowest proportion of larvae ingesting needle material during 328-384 d occurred at the clay high exposure shoreline possibly because microbial conditioning was reduced due to anaerobic conditions produced by heavy sedimentation (see Effects of shoreline type and exposure to waves, below). Leaf breakdown in anaerobic habitats does not involve aquatic hyphomycete fungi, the primary leaf conditioning organisms (Cummins 1973, 1974). A greater proportion of larvae may have been feeding at the clay low exposure shoreline than the bedrock low exposure shoreline because of the presence of slightly more sediment at the former. Richer

populations of leaf conditioning microorganisms may be found in the presence of small quantities of lake sediment than in the complete absence of sediment (Gasith and Lawacz 1976). Levels of microbial conditioning cannot be used to explain the proportions of chironomid larvae ingesting needle material at the bedrock high exposure shoreline during 328-384 d because wave action is the main determinant of breakdown at this shoreline (see Effects of shoreline type and exposure to waves, below).

The presence of P. punctipes and B. flavifrons larvae within the mesophyll region of individual needles is an indication that these larvae are mining into and consuming the needles from within. The larvae of several chironomid genera (e.g. Cricotopus, Chironomus, Endochironomus, Glyptotendipes, Polypedilum, Stenochironomus, and Stictochironomus) are known to mine vascular hydrophytes (Coffman 1978). Summerbell and Cannings (1981) found Brillia retifinis (Saether) mining into and consuming the mesophyll of Pseudotsuga menziesii (Mirb.) Franco (Douglas fir) and Taxus brevifolia Nutt. (Pacific yew) needles in a British Columbia stream. Larvae of some Brillia species also mine and aid in the breakdown of submerged wood debris (Anderson et al. 1978; Coffman 1978), but Phaenopsectra larvae are not known to be miners (Coffman 1978). In Southern Indian Lake, individuals of P. punctipes and B. flavifrons, especially those within the mesophyll region of needles, may be functioning as shredders (sensu Boling et al. 1975).

Effects of shoreline type and exposure to waves

Ranking of shorelines according to rate of needle breakdown (i.e. bedrock high exposure > clay low exposure > bedrock low exposure > clay high exposure; Table 2, Fig. 3) did not yield an obvious relation between breakdown rate and either shoreline type or wave exposure. However, individual shoreline characteristics can be used to explain these results, as follows:

(1) bedrock high exposure - Exposure to waves, in the absence of sedimentation, may have been responsible for the fastest breakdown rates at this shoreline. Meyer (1980, p. 50) recorded the fastest breakdown of leaf packs in Bear Brook, New Hampshire, at "...sites of low deposition, where scouring and physical breakup of leaves would be greatest." Webster and Waide (1982), working in Big Hurricane Branch, a second-order stream located at Coweeta Hydrologic Laboratory, North Carolina, indicated that the movement of suspended sediment particles may enhance this scouring. The effects of this exposure to waves may have been most intense during the period immediately following ice-out (\approx day 300) when the needle packs contained large amounts of material loosened by a winter of biological processing.

(2) clay high exposure - Heavy deposition of fine-grained sediments eroded from the shore by wave action were responsible for the slow breakdown rate at this shoreline. Needle packs were buried beneath 2 cm of sediment, causing compaction, decreased physical abrasion and mechanical breakage, and anaerobic conditions (Herbst 1980). Reice

(1974), Cummins et al. (1980), Meyer (1980), and Webster and Waide (1982) also observed reduced breakdown rates of leaf packs within the depositional zone of streams.

(3) clay low exposure and bedrock low exposure - These shorelines had rates of needle breakdown intermediate between the bedrock high exposure and clay high exposure shorelines. Microbial conditioning and macroinvertebrate feeding are the important factors in needle breakdown at these shorelines. The greater rate of breakdown at the clay low exposure shoreline may be in response to the presence of slightly greater amounts of sediment (see Effects of macroinvertebrates, above) than at the bedrock low exposure shoreline.

Thus, it is conceivable that physical processes, such as wave action that abrades needles and heavy sedimentation that buries them, are the main determinants of needle breakdown at high exposure shorelines. In contrast, biological processes, such as microbial conditioning and macroinvertebrate feeding, may be the main determinants of breakdown at less stressful, low exposure shorelines.

CHAPTER FOUR

MACROINVERTEBRATE COLONIZATION OF PICEA MARIANA

NEEDLE STRINGS IN SOUTHERN INDIAN LAKE, WITH SPECIAL

REFERENCE TO LARVAL CHIRONOMIDAE

INTRODUCTION

Wave exposure and sediment deposition have been shown to influence the breakdown of P. mariana needles in Southern Indian Lake (Chapter Three). These factors may also influence the abundance and community structure of macroinvertebrates colonizing the needles, either directly because of differing habitat tolerances of the colonizing macroinvertebrates (e.g. Macan 1961; Rabeni and Minshall 1977; Vaughan 1982) or indirectly because of differing physical, chemical, and/or biological conditions of the needles resulting from different rates of needle breakdown (e.g. Petersen and Cummins 1974; Sedell et al. 1975; Davis and Winterbourn 1977; Winterbourn 1978; Pidgeon and Cairns 1981). Factors involved in needle pack construction (e.g. influence of mesh bags or the oven-drying of the needles, Chapter Three) may also influence macroinvertebrate colonization of the needle strings. The first objective of this chapter was to examine the effects of wave exposure, sedimentation rate, and state of needle breakdown on macroinvertebrate colonization of the needle strings. A second objective was to examine the influence of mesh bags and oven-drying of the needles on colonization of the needle strings by macroinvertebrates.

Ephemeroptera, Trichoptera, and Plecoptera appear to be the major colonizers of leaf and needle packs in lotic systems (e.g. Petersen and Cummins 1974; Sedell et al. 1975; Davis and Winterbourn 1977; Reice 1977, 1978, 1980, 1981; Short et al. 1980; Short and Ward 1980; Pidgeon and Cairns 1981; Rosset et al. 1982). In lentic systems, however, Amphipoda, Gastropoda, and Chironomidae appear to be the major colonizers of leaf packs (Barnes et al. 1978; Webster and Simmons 1978; Hanlon 1982). Larval Chironomidae appear to be especially important in Southern Indian Lake (Chapter Three).

The Chironomidae are well adapted to exploit habitats created by the inundation of terrestrial vegetation because the family contains a large number of species which occupy virtually every type and condition of aquatic habitat (Baxter 1977; Warwick 1980). In addition, most chironomid communities contain species representing all trophic functional groups (e.g. shredders, collectors, scrapers, and predators) (Coffman 1978).

Chironomids colonize newly flooded areas rapidly. For example, stick-chain artificial substrates in newly created Lake Kariba, central Africa, were colonized by chironomid larvae within 24 h of submergence (McLachlan 1970). This colonization originates primarily from adults ovipositing within newly flooded areas or by larvae and/or egg masses drifting in from surrounding areas (McLachlan 1970; Vaughan 1982). A third objective of this chapter was, therefore, to assess the importance of macroinvertebrate colonization from these two sources compared to

colonization by macroinvertebrates already present in the bottom substrate at each of the study shorelines.

MATERIALS AND METHODS

Macroinvertebrate colonization of needle strings

Macroinvertebrates were collected from the 3 mm-mesh P. mariana needle packs used in the breakdown experiment described in Chapter Three. Three 3 mm-mesh needle packs were removed from each of the study shorelines (clay low exposure, clay high exposure, bedrock low exposure, and bedrock high exposure; Table 1) at intervals of 0 (28 July 1979), 3, 5, 13, 20, 27, 34, 41 (7 September 1979), 328 (20 June 1980), 335, 342, 356, 363, 370, 377, and 384 d (14 August 1980). Needle packs were returned to the laboratory and macroinvertebrates associated with the needle strings were live-sorted, counted, and preserved in 70% ethanol. Ostracods, copepods, and cladocerans were not enumerated because they could not be sampled quantitatively.

Most chironomid larvae were mounted on microscope slides, using polyvinyl lactophenol as a combination mounting and clearing medium (Martin 1977), to prepare them for identification. Permanent mounts of representative specimens were prepared by clearing the larvae in 10% KOH, rinsing in distilled water and then in 95% ethanol, and mounting in Euparal (Simpson and Bode 1980). The larval keys of Oliver et al. (1978) and Simpson and Bode (1980) were used to identify the chironomid larvae to genus.

A 2 x 2 factorial analysis of variance (ANOVA) blocked for sampling date (Snedecor and Cochran 1980) was used to examine differences in total numbers of macroinvertebrates colonizing needle packs according to shoreline type and exposure to wave energy. Data were transformed, using $\log_e (x+1)$, to stabilize variances.

Chironomid communities colonizing the needle strings were characterized by the numbers of taxa present and by the Shannon-Weaver (H') and Simpson (C) measures of population diversity. The Shannon-Weaver index (Poole 1974; Southwood 1978) was calculated using:

$$H' = - \sum_{i=1}^S p_i \log_e p_i$$

where S is the total number of identified taxa and p_i is the proportion of the number of individuals consisting of the i th taxon. The Shannon-Weaver index was used to measure the evenness or degree of equality of the abundances of the taxa within the communities (Poole 1974). Highest values of H' result when numbers are equally distributed among taxa. The occurrence of one exceedingly abundant taxon will result in a low H' value (Poole 1974). Simpson's measure of diversity was calculated by:

$$C = \sum_{i=1}^S \frac{n_i (n_i - 1)}{N (N - 1)}$$

where S is the total number of identified taxa, N is the total number of individuals within the community, and n_i is the number of individuals of the i th taxon. C is a measure of the probability that two

individuals in a community are of the same taxon (Poole 1974). As a result, C is most strongly affected by abundances of the one or two most dominant taxa in the community. H' and C were calculated for the 0-41 d, 328-384 d, and 0-384 d colonization periods. Kendall's "Tau" (τ) coefficient (Ghent 1963) was used as an index of similarity for comparing chironomid communities at the different shorelines during both 0-41 and 328-384 d periods. Communities were judged to be similar if $p < 0.01$.

Benthic vs planktonic colonization

The P. mariana needle packs used in this experiment were identical in construction to the 3 mm-mesh packs used in the breakdown experiment (Chapter Three). They were placed, using SCUBA, at the clay low exposure shoreline on 27 June 1980. Thirty needle packs were anchored in contact with the substrate (benthic packs) in 2 mm of water, and 30 additional packs were suspended in the water column (suspended packs) 1 m directly above the benthic packs (Fig. 6). The suspended packs could be colonized only by planktonic organisms whereas the benthic packs could be colonized by both benthic and planktonic organisms.

Three benthic and three suspended packs were removed, using SCUBA, at intervals of 7 (4 July 1980), 21, 28, 35, 42, and 49 d (15 August 1980). They were returned to the laboratory and the associated macroinvertebrates removed and counted. A two-way ANOVA (Snedecor and Cochran 1980) was used to examine differences in numbers of

macroinvertebrates colonizing the benthic and suspended packs. Factors used were pack type (benthic vs suspended) and sampling date.

Checks on experimental methods

To examine the influence of mesh bags and oven-drying of the needles on the macroinvertebrate colonization of the P. mariana needle strings, empty 3 mm-mesh bags, identical to those used in the breakdown experiment (Chapter Three), and 3 mm-mesh packs containing strings of fresh (not oven-dried) P. mariana needles were anchored on the substrate, using SCUBA, in 2 m of water at the clay low exposure shoreline. The packs and mesh bags were installed on 27 June 1980. At intervals of 7 (2 July 1980), 21, 28, 35, 42, and 49 d (15 August 1980), three packs and three mesh bags were removed, using SCUBA, and returned to the laboratory where macroinvertebrates were removed and counted.

Two-way ANOVA's (Snedecor and Cochran 1980) were used to examine: (1) differences in numbers of macroinvertebrates colonizing the mesh bags and the benthic packs installed at the same time (see above), and (2) differences in numbers of macroinvertebrates colonizing packs containing fresh and oven-dried (benthic packs, see above) needle strings. Factors used were treatments (mesh bag vs needle pack; fresh vs oven-dried needle strings) and sampling date. The benthic packs were used as a control.

RESULTS

Macroinvertebrate numbers

Macroinvertebrate colonization (number per string, number per gram final needle string dry weight) of the 3 mm-mesh needle packs used in the breakdown experiment (Chapter Three) began within 3 d of their installation and increased throughout the initial 41 d of the experiment (Figs. 4 and 5). Needle strings at low exposure shorelines were colonized by higher numbers of macroinvertebrates than needle strings at high exposure shorelines (Figs. 4 and 5). This difference was significant at 34 d and 41 d but not before these times (Table 4). Numbers of macroinvertebrates were not influenced by clay or bedrock shoreline types at any time during the 0-41 d colonization period (Table 4).

Mean numbers of macroinvertebrates per needle string declined to <20 between 41 and 328 d at the clay shorelines and to <10 at the bedrock shorelines (Fig. 4). The mean number of macroinvertebrates per gram of final needle string dry weight increased at the clay low and bedrock high exposure shorelines between 41 and 328 d but remained at levels similar to 41 d at the clay high and bedrock low exposure shorelines (Fig. 5).

During the 328-384 d colonization period, mean numbers per string increased and then declined at all shorelines except bedrock high exposure where mean numbers remained <10 (Fig. 4). Mean numbers of macroinvertebrates per gram of needles showed a general increase at all

shorelines during the same period (Fig. 5). Maximum numbers per gram occurred at the clay low and bedrock high exposure shorelines, while minimum numbers per gram occurred at the clay high exposure shoreline. The bedrock low exposure shoreline was intermediate but more clearly resembled the clay high exposure shoreline. Shoreline type and wave exposure significantly influenced mean numbers of macroinvertebrates per needle string during the 328-384 d period, while only wave exposure significantly influenced macroinvertebrate numbers per gram during the same period (Table 4). The interaction term was significant for both measures. The results of analyses done for 0-384 d duplicated those obtained for the 328-384 d period (Table 4).

Macroinvertebrate taxa

Larval Chironomidae comprised >50% of the macroinvertebrates colonizing needle strings over the 384 d study period. Large macroinvertebrates, such as Ephemeroptera (Baetis), Trichoptera (Polycentropus, Phryganea, Lepidostoma), and Plecoptera, never exceeded three individuals per needle string. Small numbers of the amphipod Pontoporeia brevicornis grp. also were found. Nematoda, Oligochaeta, Hydracarina, Saldidae (Hemiptera), and larval Ceratopogonidae (Diptera) were infrequently found and were not identified to lower taxonomic levels.

Twenty-seven taxa of chironomidae were identified over the 384 d of the study, including six taxa of Tanypodinae, seven taxa of

Orthocladiinae, 10 taxa of Chironomini, and four taxa of Tanytarsini (Table 5). Over 50% of the larvae from each shoreline were Chironomini (Fig. 7). Mean numbers per string of Tanypodinae, Orthocladiinae, and Tanytarsini were similar (≤ 1 individual per needle string) at all shorelines except the bedrock high exposure. At this shoreline, Tanypodinae were poorly represented during the entire study (0-384 d) while the numbers of Tanytarsini were low during the 0-41 d period but were approximately equal to those of the Orthocladiinae during 328-384 d.

Only six taxa (Ablabesmyia, Microtendipes, Parachironomus, Phaenopsectra punctipes (Wied.), Cladotanytarsus, and Tanytarsini genus 1) were present at all four shorelines during both the initial (0-41 d) and final (328-384 d) colonization periods (Table 5). Most taxa were found at each shoreline at least once over the duration of the study, although many were present only in very low numbers (e.g. ≤ 0.1 individuals per needle string) (Table 5). Some taxa were found only at three of the four shorelines (e.g. Cricotopus and Glyptotendipes, absent from clay high exposure; Tanypodinae genus 1 and Psectrocladius, absent from bedrock high exposure) while others were restricted to one shoreline (e.g. Paratanytarsus at clay low exposure; Stempellinella at clay high exposure; Thiennemannimyia (T.) norena (Rob.) at bedrock high exposure), one shoreline type (e.g. Tanypodinae genus 3 at clay shorelines), or one wave exposure (e.g. Orthocladius, Cryptochironomus, and Endochironomus nigricans (Joh.) at low wave exposure shorelines) (Table 5).

P. punctipes was the most abundant chironomid at the clay low exposure and bedrock low exposure shorelines during the 0-41 d, 328-384 d, and 0-384 d colonization periods, accounting for 31-55% of the identified larvae (Table 6). It was also the most abundant chironomid at the bedrock high exposure shoreline during the 0-41 d and 0-384 d periods, accounting for 49% and 37% of the identified larvae respectively. Parachironomus was the most abundant taxon at the bedrock high exposure shoreline during 328-384 d (47% of the larvae from the shoreline). Microtendipes was the dominant chironomid at the clay high exposure shoreline during 0-41 d and 0-384 d (40% and 30% of the larvae), whereas Procladius was dominant during the 328-384 d period (26% of the larvae). Other numerically important taxa include: Ablabesmyia at the clay low exposure, clay high exposure, and bedrock low exposure shorelines; Corynoneura at the bedrock high exposure shoreline; Chironomus at the bedrock low and high exposure shorelines; Cladotanytarsus at the bedrock high exposure shoreline; and Tanytarsini genus 1 at the clay low exposure, clay high exposure, and bedrock low exposure shorelines (Table 6).

Characterization and comparison of chironomid communities

The chironomid communities colonizing P. mariana needle strings are characterized in Table 7. Initially (0-41 d), similar numbers of taxa were present at all shorelines except bedrock high exposure where the number of taxa present was lower. Numbers of taxa present at clay low

and bedrock low exposure shorelines during 328-384 d were similar to 0-41 d levels while numbers present at clay high and bedrock high exposure shorelines were lower than 0-41 d levels.

Values of the Shannon-Weaver diversity index (H') were consistently lower at clay low and bedrock high exposure shorelines than at clay high and bedrock low exposure shorelines throughout the study. Values of H' calculated for 328-384 d were higher than 0-41 d values at all shorelines except bedrock high exposure. In contrast to values of H' , values of Simpson's diversity measure (C) were consistently greater at the clay low and bedrock high exposure shorelines than at the clay high and bedrock low exposure shorelines throughout the study.

Chironomid communities at the bedrock high exposure shoreline differed from all other shorelines during the initial colonization period (0-41 d) (Table 8). During the final colonization period (328-384 d), only communities colonizing needle strings at the clay high and bedrock low exposure shorelines appeared to be similar (Table 9).

Benthic vs planktonic colonization

Macroinvertebrate colonization of the benthic and suspended needle packs increased during the initial 35 d of the study and then began to decline (Fig. 8). Numbers of macroinvertebrates colonizing the benthic packs were consistently greater than numbers colonizing the suspended packs. This difference was significant (ANOVA, $p < 0.05$; Snedecor and Cochran 1980).

Colonization of the suspended packs was mainly due to very small (presumably first instar) Chironomidae. Oligochaeta, small Ephemeroptera, larval Ceratopogonidae, and larval Coleoptera were present but their numbers rarely exceeded 1-2 individuals per string.

Over 80% of the colonization of the benthic packs was due to both early and late instar chironomid larvae. Ephemeroptera, larval Coleoptera, Oligochaeta, and Hydracarina were present in low numbers.

Checks on experimental methods

Numbers of macroinvertebrates colonizing the empty mesh bags remained stable and never exceeded a mean of 10.3 individuals per bag (Fig. 8). Numbers of macroinvertebrates colonizing the empty bags were significantly lower (ANOVA, $p < 0.01$; Snedecor and Cochran 1980) from the number colonizing the benthic needle packs (Fig. 8). Chironomid larvae represented over 80% of the macroinvertebrates colonizing the empty bags.

Colonization of the packs containing the fresh (not oven-dried) needles increased over the initial 28 d of the study and then declined (Fig. 8). Mean numbers of macroinvertebrates colonizing the fresh needle strings were not significantly different (ANOVA, $p > 0.05$; Snedecor and Cochran 1980) from numbers colonizing the oven-dried needle strings contained within the benthic packs (Fig. 8). Chironomid larvae represented over 80% of the macroinvertebrates colonizing the fresh needle strings.

DISCUSSION

Macroinvertebrate numbers and community structure

It is difficult to identify any sequences of macroinvertebrates colonizing the needle strings in Southern Indian Lake because most taxa are represented by very low numbers of individuals (Table 5). However, differences in wave exposure, sedimentation rate, and the amounts of needle material remaining can be used to explain both the numbers of colonizing macroinvertebrates (Figs. 4 and 5) and the structure of the chironomid communities (represented by the most abundant taxa at each shoreline, Tables 5 and 6) during the initial (0-41 d) and final (328-384 d) colonization periods. This evidence is as follows:

(1) wave exposure - During 0-41 d, lower numbers of colonizing macroinvertebrates at the bedrock high exposure shoreline compared to the bedrock low exposure shoreline (mean numbers per string 15.0 and 18.8, respectively; Fig. 4), and the dissimilarity of chironomid communities at the bedrock high exposure shoreline to communities at any of the other shorelines (Table 8) may be due to decreased habitat stability caused by intense wave action at the bedrock high exposure shoreline. Similar effects of intense wave action on macroinvertebrate communities have been observed in Georgian Bay, Lake Ontario (Barton and Carter 1982); Cow Green reservoir (Armitage 1977); and along marine subtidal beaches (Oliver et al. 1980). Many taxa abundant within low wave exposure areas are not tolerant of high wave energies, and as a result, are often not abundant within high wave exposure areas (Oliver

et al. 1980; Barton and Carter 1982). Alternatively, other taxa are abundant only within high exposure areas, possibly because of the lack of potential predators and/or competitors capable of tolerating high wave energy conditions (Oliver et al. 1980; Barton and Carter 1982). In Southern Indian Lake during 0-41 d, lower numbers of Tanypodinae and Tanytarsini colonized needle strings at the bedrock high exposure shoreline compared to the bedrock low exposure shoreline (Fig. 7) indicating these two groups may not be very tolerant of high wave energies. Barton and Carter (1982) found these groups were also absent from high wave energy shorelines in Georgian Bay, Lake Ontario. Abundances of Ablabesmyia, Procladius, and Tanytarsini genus 1 appear to have been most affected by conditions present at the bedrock high exposure shoreline (Table 5). Slightly higher numbers of Orthocladiinae colonized needle strings at the bedrock high exposure shoreline compared to the bedrock low exposure shoreline (Fig. 7) indicating that abundance of this group may have been enhanced by wave conditions present at the high exposure shoreline. Corynoneura and Cricotopus appear to have been most enhanced (Table 5). Total numbers of Chironomini at the bedrock high and low exposure shorelines during 0-41 d showed no effect of wave action (Fig. 7), however, individual taxa within the group show a variety of responses to the high wave energies present at the high exposure shoreline (Table 5). Abundances of Cryptochironomus, Glyptotendipes, Microtendipes, and Polypedilum appear to have been reduced at the high exposure whereas the abundance of Paratendipes was

increased. Chironomus, Dicrotendipes, Parachironomus, and P. punctipes appear not to have been affected by high wave energies. The dissimilarity of chironomid communities at the bedrock high exposure shoreline to communities at any of the other shorelines during 0-41 d (Table 8) appears to be mainly due to the decreased abundances of Ablabesmyia, Microtendipes, and Tanytarsini genus 1 and, perhaps, to the increase in abundance of Paratendipes at the bedrock high exposure shoreline (Table 6). Decreased abundances of Ablabesmyia, Microtendipes, and Tanytarsini genus 1 also appear to account for the lower value of H' and the higher value of C at the bedrock high exposure shoreline compared to the bedrock low exposure shoreline during 0-41 d (Table 7).

High wave energies may also have influenced the structure of chironomid communities at the clay high and bedrock high exposure shorelines during the 328-384 d period. However, no trends can be identified because this influence is obscured by heavy sediment deposition at the clay high exposure shoreline and by the small amounts of needle material remaining at the bedrock high exposure shoreline (see below).

(2) sedimentation rate - Lower numbers of macroinvertebrates colonizing needle strings at the clay high exposure shoreline compared to the clay low exposure shoreline (Figs. 4 and 5) may be due to the effects of intense sedimentation at the high exposure shoreline. High sedimentation rates have been shown to cause substrate instability and

smothering of benthic macroinvertebrates (Hynes 1973; Rosenberg and Snow 1975; Allen and Hardy 1980). Many taxa of Chironomidae are sensitive to the effects of sedimentation and may become reduced in abundance or eliminated by excessive sedimentation (Warwick 1980). Other taxa appear to be favored by sedimentation and may increase in abundance (Warwick 1980). Predatory taxa appear to be especially favored because their prey are forced to the surface by unstable bottom conditions and are easier to find (Warwick 1980). In Southern Indian lake, Orthocladiinae colonizing the needle strings appeared to be especially reduced in abundance due to the effects of sedimentation at the clay high exposure shoreline compared to the clay low exposure shoreline (Fig. 7). Total numbers of Tanytarsini and Chironomini colonizing needle strings in Southern Indian Lake did not appear to be affected by sedimentation at the clay high exposure shoreline (Fig. 7), however, individual taxa of Chironomini showed a variety of responses to the sedimentation (Table 5). For example, P. punctipes appeared to have a low tolerance to sedimentation because fewer were present at the clay high exposure than at the clay low exposure shoreline. Microtendipes appeared to be favored by sedimentation because its greatest abundance occurred at the clay high exposure shoreline compared to any of the other shorelines. Chironomus and Parachironomus showed no response to the effects of sedimentation. The responses of other taxa of Chironomini are difficult to determine because of the low numbers in which they were found. Most Tanypodinae did not show any response to sedimentation at the clay high

exposure shoreline (Fig. 7; Table 5), however, Procladius appeared to be greatly favored by sedimentation during the final colonization period (328-384 d), possibly because prey which were forced to the sediment surface by unstable bottom conditions were easier to locate (see above). Procladius did not appear to be favored by sedimentation at the clay high exposure shoreline during 0-41 d, possibly because the amount of sediment deposited onto the needle strings during this period ($\approx 1-3$ mm) was not enough to give Procladius a competitive advantage over any other taxa. Reduction in the abundance of P. punctipes and increase in the abundance of Procladius are probably responsible for the lack of similarity of chironomid communities at the clay high exposure shoreline during 328-384 d to all other shorelines except bedrock low exposure (Table 9). The similarity of communities at the clay high and bedrock low exposure shorelines appears to be due to the high abundance of Procladius at both shorelines (Tables 5 and 6), due to easy location of prey at both shorelines. Prey would have been easy to locate at the bedrock low exposure shoreline because only a thin layer of sediment overlying the bedrock (≈ 1 cm) was available to burrowing taxa.

(3) amount of needle material remaining - During the final colonization period, mean numbers of macroinvertebrates per g of needle material remaining (Fig. 5) can be ranked similarly to rates of needle breakdown (Fig. 3, Table 2) except that macroinvertebrate numbers at the bedrock high and clay low exposure shorelines are reversed (i.e. mean numbers of macroinvertebrates per g of needle material remaining: clay high

exposure < bedrock low exposure < bedrock high exposure < clay low exposure). There are two possible explanations for this observed sequence: (1) the extent of microbial conditioning (Petersen and Cummins 1974), and (2) the amount of needle material remaining (Davis and Winterbourn 1977; Winterbourn 1978). Numbers of macroinvertebrates per needle string (Fig. 4) during 328-384 d were similar at all shorelines except bedrock high exposure where numbers were less than at the other shorelines. In addition, amounts of colonizable needle material were lower at the bedrock high exposure (<5% of the initial dry weight, Fig. 3) than at the other shorelines during this period. This indicates that colonization of the needles during 328-384 d was primarily a function of the amount of needle material remaining and not the extent of microbial conditioning. Davis and Winterbourn (1977) and Winterbourn (1978) reported similar results for the macroinvertebrate colonization of Nothofagus spp. (beech) leaves in New Zealand streams. The low numbers of Heterotrissocladius changi Saether and Chironomini, including Chironomus, Dicrotendipes and P. punctipes, colonizing needle strings at the bedrock high exposure shoreline during 328-384 d compared to 0-41 d (Table 5) support this finding. This difference, along with the low numbers of colonizing Tanypodinae at the bedrock high exposure shoreline probably also accounts for the dissimilarity of chironomid communities between this shoreline and others (Table 9).

Benthic vs planktonic colonization

The macroinvertebrate colonization of benthic and suspended needle packs (Fig. 8) indicates that the colonization of P. mariana needles in Southern Indian Lake is due to both macroinvertebrates in the surrounding substrate and to macroinvertebrates, mostly first instar chironomid larvae, drifting within the water column. The planktonic portion of this colonization would be most important within newly-flooded areas where macroinvertebrates have not had time to sufficiently colonize the surrounding bottom substrate. Higher numbers of macroinvertebrates were found colonizing the benthic packs because they were subject to colonization from both the substrate and the water column whereas the suspended packs could be colonized only by planktonic organisms.

Checks on experimental methods

Similar numbers of macroinvertebrates colonizing packs containing either fresh or oven-dried needles indicates that drying did not influence colonization of the needle strings. As a result, except for the possible exclusion of large macroinvertebrates by the 3 mm-mesh (see Chapter Three), conditions in the needle packs used in this study were probably similar to those found within natural accumulations of P. mariana needles in Southern Indian Lake.

Significantly higher numbers of macroinvertebrates were found on benthic needle packs compared to the empty 3 mm-mesh bags, which

indicates that macroinvertebrates selectively colonized the P. mariana needles. Thus, the macroinvertebrates were attracted by a food source and not simply by a refuge. Pidgeon and Cairns (1981) also found that the numbers of macroinvertebrates were consistently higher in bags containing leaves than in empty bags or those containing plastic strips.

CHAPTER FIVE
THE SIGNIFICANCE OF PICEA MARIANA NEEDLE ADDITION
TO SOUTHERN INDIAN LAKE

INTRODUCTION

Inundated vegetation in new reservoirs serves not only as an important source of energy and organic matter to aquatic food chains but also is often the most abundant habitat available for macroinvertebrate colonization (McLachlan 1970). Nutrients released by the breakdown of inundated vegetation are thought to contribute to the trophic upsurge commonly observed in many new reservoirs (see review by Baxter 1977). For example, Ostrofsky (1978) developed a model that incorporated the leaching rates of phosphorus from inundated vegetation, and was able to calculate phosphorus concentrations accounting for the trophic upsurge phases observed in several temperate region reservoirs.

McLachlan (1977) found terrestrial vegetation to be the major source of food for macroinvertebrates in new tropical and temperate reservoirs. These macroinvertebrates, in turn, may serve as important fish food organisms (Cherry and Guthrie 1975). Thus, large inputs of terrestrial vegetation due to impoundment can increase the production of macroinvertebrate fish food organisms resulting in increased production of fish within the new reservoir (Cherry and Guthrie 1975).

The objectives of this chapter were as follows: (1) to estimate the biomass of P. mariana needles inundated by the impoundment of

Southern Indian Lake; (2) to estimate the quantities of C, N, and P released by the breakdown of the inundated needles; and (3) to estimate the importance of P. mariana needles as a habitat for colonization by potential macroinvertebrate fish food organisms.

Calculations

The biomass (kg dry wt m^{-2}) of P. mariana needles inundated by the flooding of Southern Indian Lake was estimated as follows:

(1) P. mariana trunk diameters were measured in seven plots at three representative shorelines on the lake (D.M. Rosenberg and A.P. Wiens, Freshwater Institute, Winnipeg, Manitoba, unpubl. data).

(2) The biomass of needles on each tree was calculated using the regression formula of Weetman and Harland (1964):

$$\log_{10} (W) = 3.2377 \log_{10} (D) - 1.7836$$

where

W = needle biomass (kg)

D = tree trunk diameter (inches).

(3) An average biomass m^{-2} of needles was calculated for each plot and then the seven plots overall, and this average was multiplied by the total area of shoreline flooded (346 km^2).

Potential nutrient inputs (I_p)

Potential inputs of C, N, and P to Southern Indian Lake resulting from the complete breakdown of all inundated P. mariana needles were

estimated from needle nutrient concentrations of $419 \mu\text{g C mg}^{-1}$, $5.24 \mu\text{g N mg}^{-1}$, and $0.62 \mu\text{g P mg}^{-1}$ dry weight (G.K. McCullough, Freshwater Institute, and J.M. Shay, Dept. of Botany, University of Manitoba, Winnipeg, Manitoba, unpubl. data).

Actual nutrient inputs (I_A)

Actual inputs of C, N, and P from needle breakdown during the first year following flooding (1977) were estimated by the negative exponential equation (cf Jenny et al. 1949; Petersen and Cummins 1974):

$$I_A = I_p (1 - e^{-kt})$$

where

I_A = estimated actual input

I_p = estimated potential input

e = base of the Naperian logarithm

k = mean breakdown coefficient (0.0057 d^{-1} , Table 2)

t = time (365 d).

The following assumptions were made:

- (1) All needles were inundated simultaneously.
- (2) All inundated needles remained within the flooded terrestrial area.
- (3) All needles were broken down at the same exponential rate (k).
- (4) C, N, and P were released at the same rate as the needles were broken down.
- (5) Needle breakdown and nutrient input were essentially completed by 365 d.

Importance to macroinvertebrates

To assess the importance of P. mariana needle addition and breakdown to macroinvertebrate populations in Southern Indian Lake, the potential number of macroinvertebrates colonizing inundated needles was calculated by multiplying the estimated mean density of macroinvertebrates g^{-1} needles during the first year after flooding (1977) by the weight of needles estimated to have been inundated (see above). The following assumptions were required:

- (1) All inundated needles were inundated simultaneously.
- (2) All inundated needles remained within the flooded terrestrial area.
- (3) All inundated needles were equally accessible to macroinvertebrate colonization.
- (4) The mean density of macroinvertebrates colonizing inundated needles during the first year is represented by the mean density of macroinvertebrates colonizing the needles over the duration of the present study (61.5 macroinvertebrates g^{-1} needles; see also Fig. 5).

RESULTS

Needle biomass and nutrient inputs

The impoundment of Southern Indian Lake inundated $\approx 5.4 \times 10^5$ tonnes of P. mariana needles. Complete breakdown of these needles could potentially release 2.28×10^5 tonnes C, 2.85×10^3 tonnes N, and 3.37×10^2 tonnes P to aquatic food chains within the reservoir (Table 10). Using the assumptions made and a mean breakdown rate of $0.0057 d^{-1}$ (mean

for 0-384 d, Table 2), 87.5% [i.e. $(1 - e^{-kt}) \times 100\%$] of all inundated needle biomass would be broken down within 365 d of inundation, releasing 2.00×10^5 tonnes C, 2.49×10^3 tonnes N, and 2.95×10^2 tonnes P (Table 10).

Potential numbers of macroinvertebrates colonizing needles

It was estimated that a total of 3.3×10^{13} macroinvertebrates colonized the 5.4×10^5 tonnes of inundated P. mariana needles in Southern Indian Lake (61.5 macroinvertebrates g^{-1} needles $\times 5.4 \times 10^{11}$ g needles). Density of the macroinvertebrates colonizing needles within the flooded terrestrial area (346 km^2) would have been $96,000$ macroinvertebrates m^{-2} .

DISCUSSION

Significance of needle addition

The estimated actual inputs of C (2.00×10^5 tonnes), N (2.49×10^3 tonnes), and P (2.95×10^2 tonnes) due to the breakdown of inundated P. mariana needles (Table 10) are low compared to the total amounts contained within all of the inundated vegetation (5.87×10^6 tonnes C, 1.70×10^4 tonnes N, and 2.57×10^3 tonnes P; G.K. McCullough and J.M. Shay, unpubl. data). However, the estimated 83 g C m^{-2} of lake surface (Table 10) is higher than the annual primary productivity measured for 1977 ($\approx 55 \text{ g C m}^{-2} \text{ yr}^{-1}$; Hecky and Guildford 1984), the first year following impoundment. These estimated inputs are also

considerably higher than the average amounts of C ($\approx 14 \text{ g m}^{-2}$), N ($\approx 0.24 \text{ g m}^{-2}$), and P ($\approx 0.005 \text{ g m}^{-2}$) within Southern Indian Lake during the 1977 open-water season (R.E. Hecky, Freshwater Institute, Winnipeg, Manitoba, unpubl. data). Thus, P. mariana needle breakdown in Southern Indian Lake may have been an important short-term source of nutrients and energy to aquatic food chains within the reservoir, although it is not known what quantities of nutrients released from the P. mariana needles were actually used for 1° and 2° production within the lake. Rau (1980), using carbon ratios ($^{13}\text{C}/^{12}\text{C}$), attributed 38% of the biomass of insects emerging from Findley Lake, Washington, to allochthonous vegetation, mainly conifer needles.

Density of the macroinvertebrates colonizing P. mariana needles within the flooded terrestrial area was estimated to be 96,000 macroinvertebrates m^{-2} , a figure much higher than the 2500-4000 macroinvertebrates m^{-2} obtained in the 0-5 m depth zone by Wiens and Rosenberg (1984) during 1972, 1977, and 1979 surveys of the lake. Moreover, the 96,000 m^{-2} figure could not be checked directly because needles either were broken down within one year of inundation or were buried by heavy sediment deposition. As a result, natural accumulations of needles could not be sampled.

Violation of the assumptions

The estimates of actual inputs of C, N, and P from needle breakdown, and of the potential number of macroinvertebrates colonizing

the inundated needles may be inaccurate, for the following reasons:

- (1) All needles were not inundated simultaneously but were shed from inundated trees over a period of more than a year (G.K. McCullough, pers. comm.). As a result, both the amounts of nutrients added and the number of colonizing macroinvertebrates were probably overestimated.
- (2) There may have been losses of incompletely broken down needle fragments from the packs which were included in the calculations of k (see also Chapter Three). As a result, actual nutrient inputs appear to be overestimates.
- (3) All leaf constituents (e.g. sugars, lipids, proteins, waxes, cellulose, and lignin) are not broken down at the same rate as weight is lost from leaf packs (e.g. Minderman 1968; Suberkropp et al. 1976). Therefore, C, N, and P may not have been released at the same rate as the needles were broken down. However, summation of the exponential curves representing the breakdown of the individual leaf constituents produces a curve that closely approximates total leaf weight losses (Minderman 1968). This indicates that the rate of weight loss (k) represents the average breakdown rate of all leaf components and, although C, N, and P may be released at different rates, k is probably also a fair representation of the average of nutrient release.
- (4) Amounts of N and P present in leaf material often remain stable or increase (e.g. Howarth and Fisher 1976; Suberkropp et al. 1976; Meyer 1980), apparently indicating that the release of these nutrients cannot be represented by the negative exponential model. It has been found,

however, that increased levels of N and P present in leaf material are due to the microbial fixation of inorganic N and P from the surrounding water and sediments (Kaushik and Hynes 1971; Howarth and Fisher 1976; Suberkropp and Klug 1976; Meyer 1980). In fact, microbial fixation of N and P may ultimately increase the absolute amounts of these nutrients released to macroinvertebrate populations because such enriched leaf material is highly conditioned (see Chapter Three) and will be a preferred food source (Kaushik and Hynes 1971; Bärlocher and Kendrick 1975; Bärlocher et al. 1978a; Summerbell and Cannings 1981). As a result, use of the exponential model is actually a conservative estimate of the release of C, N, and P by needle breakdown.

The first two violations listed above [i.e. (1) all needles were not inundated simultaneously; (2) incompletely broken down needle fragments were lost from the packs] are the most serious, resulting in overestimates of both the amounts of C, N, and P added and the numbers of colonizing macroinvertebrates. However, the other two violations [i.e. (3) C, N, and P are not released at the same rate as the needles were broken down; (4) N and P are not released exponentially] are not serious, indicating that the use of the exponential model to calculate nutrient release during needle breakdown is valid.

CHAPTER SIX

GENERAL DISCUSSION

PARTITIONING OF NEEDLE STRING WEIGHT LOSSES

Inundated Picea mariana needles in Southern Indian Lake are broken down by leaching, microbial conditioning, macroinvertebrate feeding, and abrasion due to wave action (see Chapter Three). Sediment deposition, however, can inhibit both microbial and macroinvertebrate processes (see Chapters Three and Four), resulting in slower rates of needle breakdown. The experimental design of this study (see Chapter Three and below) allows the enhancement or inhibition of needle string weight losses to be partitioned from total weight losses at each shoreline by using graphical comparisons of weight loss regressions ($\log_e \% R$ vs time; 0-41 d and 328-384 d) (Fig. 9). The following assumptions were required:

- (1) Leaching was essentially complete by 3 d and represented 25% of the initial needle string dry weight (see Chapter Three).
- (2) Microbial conditioning began at 3 d (see Chapter Three).
- (3) Weight losses due to leaching and microbial conditioning during 328-384 d were represented by the regression for weight loss from the 50 μm -mesh packs.
- (4) Macroinvertebrate feeding on needle strings did not begin until the needles were sufficiently conditioned (>41 d; see Chapter Three).
- (5) High and low exposure shorelines of the same shoreline type differed only with respect to wave action and/or sediment deposition.

During 0-41 d, weight losses were similar among shorelines and pack mesh sizes, allowing one set of regressions to represent all weight losses (Column 1, Fig. 9). Leaching accounted for all weight losses up to 3 d, whereas both leaching and microbial conditioning accounted for weight losses during 3-41 d.

Leaching and microbial conditioning accounted for all weight losses from the 50 μ m-mesh packs during 328-384 d (Column 2, Fig. 9). By 384 d, leaching and microbial conditioning had accounted for almost equal amounts of weight losses.

Weight losses from the clay low exposure 3 mm-mesh packs during 328-384 d were due to leaching, microbial conditioning, and macroinvertebrate feeding (Column 3, Fig. 9). By 384 d, macroinvertebrates had accounted for almost 50% of the weight loss, while leaching and microbial conditioning each accounted for \approx 25%. Weight loss at the clay high exposure shoreline during the same period was also due to leaching, microbial conditioning, and macroinvertebrate feeding (Column 4, Fig. 9). However, deposited sediments covering these packs inhibited both microbial and macroinvertebrate processing (see Chapters Three and Four), making their contributions to needle string weight loss impossible to partition. By 384 d, 34% of the expected weight loss (based on weight loss at the clay low exposure shoreline and indicated by the dashed line in Column 4, Fig. 9) had been inhibited by sediment deposition.

Weight loss at the bedrock low exposure shoreline for 328-384 d was due to leaching, microbial conditioning, and macroinvertebrate feeding

in approximately equal proportions (Column 5, Fig. 9). Weight loss at the bedrock high exposure shoreline during 328-384 d was similar to that at the bedrock low exposure shoreline except for an additional contribution made by wave action (Column 6, Fig. 9). By 384 d, wave action had enhanced breakdown by 18% over that observed at the bedrock low exposure shoreline.

Average contributions to needle string breakdown in the 3 mm-mesh packs by each factor can be estimated for the entire study period. Leaching and microbial conditioning each accounted for $\approx 30\%$ of the weight losses, while macroinvertebrate feeding accounted for $\approx 40\%$. By comparison, Cummins et al. (1973) and Petersen and Cummins (1974) estimated that 10-15%, 22-35%, and 20-21% of the weight loss from leaves in streams was due to leaching, microbial conditioning, and macroinvertebrate feeding, respectively. Differences between these studies and the present one are probably due to differences in the species of leaves used, the macroinvertebrate communities present and, especially, the duration of the studies. Leaves should become more palatable to macroinvertebrates as breakdown proceeds because of higher levels of microbial conditioning and, as a result, the contribution made by macroinvertebrate feeding to breakdown will increase as time proceeds (e.g. Kaushik and Hynes 1971; Bärlocher and Kendrick 1975; Bärlocher et al. 1978a; Bärlocher and Rosset 1981; Summerbell and Cannings 1981; also see Fig. 9). The present study lasted longer (384 d) than either of the other two studies (30-126 d), resulting in a higher contribution by macroinvertebrate feeding.

High wave energies in Southern Indian lake may enhance total breakdown by as much as 18% while sediment deposition can inhibit total breakdown by as much as 30% (Columns 4 and 6, Fig. 9). Herbst (1980) found that burial of leaves in stream sediments could inhibit breakdown by 17-37% over a one year period.

COMPARISON OF P. MARIANA BREAKDOWN WITH OTHER PUBLISHED RESULTS

Breakdown coefficients for P. mariana needles in Southern Indian Lake are lower than those recorded for deciduous leaves in streams (range 0.0024-0.0305 d^{-1} ; Petersen and Cummins 1974; Sedell et al. 1975) and within the range of those recorded for deciduous leaves in lentic systems (range 0.00076-0.0512 d^{-1} ; Barnes et al. 1978; Hanlon 1982). Compared to other studies of the breakdown of conifer needles, breakdown coefficients for Southern Indian Lake most resemble those reported for streams, and are faster than those in other lentic systems (Table 11). Thus, it appears that wave action may be of considerable importance to needle breakdown in Southern Indian Lake, but it is of less importance in the studies of other lentic systems cited in Table 11 (Hodkinson 1975a; Rau 1978) because of the small size of the systems involved. However, caution must be used in making these comparisons because of differences in experimental design (e.g. type of leaf or needle pack used, duration of study) and the chemical composition of the leaf and needle species used.

CONCLUSIONS

The following conclusions may be drawn about the breakdown of P. mariana needles in Southern Indian Lake:

(1) The needle packs used in this study are useful for measuring the breakdown of P. mariana needles. It must be remembered, however, that needle string weight losses do not measure the extent of conversion of this material to microbial and animal biomass and CO₂.

(2) The needle packs used in this study are useful for observing the colonization of P. mariana needles by aquatic macroinvertebrates. However, larger quantities of needles should be used in order to increase the numbers of colonizing macroinvertebrates, thereby making it possible to recognize any successional trends of the taxa involved.

(3) The breakdown of P. mariana needles is a two-stage process. The initial stage depends upon leaching and microbial conditioning. The second stage depends mainly upon macroinvertebrate feeding at low exposure shorelines and upon wave action at high exposure shorelines. Heavy sediment deposition at any shoreline can inhibit the breakdown process.

(4) The colonization of inundated P. mariana needles is mainly by chironomid larvae present either in the substrate or in the water column. The planktonic portion of this colonization would be most important within newly flooded areas where macroinvertebrates have had insufficient time to colonize the substrate.

(5) Heavy wave action, heavy sediment deposition, and the reduction of

needle surface area as breakdown proceeds reduce the numbers of colonizing macroinvertebrates and can cause shifts in the structure of colonizing chironomid communities. When large amounts of needle material are present, P. punctipes is the dominant colonizer at all shorelines except those with heavy sediment deposition. At such shorelines, numbers of P. punctipes are low and Microtendipes and Procladius dominate.

(6) P. mariana needle breakdown in Southern Indian Lake may have released significant amounts of C, N, and P within localized areas during 1977, the first year following flooding, thus constituting an important short-term source of energy and nutrients to aquatic food chains within the lake. The breakdown of needles that have either become exposed after being buried by sediment deposition or have entered the lake because of shoreline erosion after impoundment may constitute a minor long-term source of energy and nutrients to the lake. In contrast, breakdown of the extremely large quantities of flooded woody debris, which may take up to 200 yr (Anderson et al. 1978), is a more important long-term source of energy and nutrients to the lake.

(7) Inundated P. mariana needles may have served as a suitable substrate for macroinvertebrate colonization, thereby temporarily increasing the population of potential fish food organisms within the lake. It is possible that additions of deciduous leaves and/or conifer needles could be used to increase macroinvertebrate fish food populations, and that these additions could be used as a tool to manage the fish stocks of lakes and reservoirs.

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Table 1. Shorelines in Southern Indian Lake used for measuring breakdown rates in experimental Picea mariana needle packs.

Shoreline type	Wave exposure	Mean erosion rate ^a (m ³ m ⁻¹ shoreline)	Mean wind-wave energy ^b (tonne-m season ⁻¹ m ⁻¹)
clay	low	0.7	1052
	high	4.1	8431
bedrock	low	assumed negligible	1570
	high	assumed negligible	11640

^a from Newbury et al. (1978).

^b Calculated for 28 September 1978 to 30 August 1980 (G.K. McCullough, Freshwater Institute, Winnipeg, Manitoba, unpubl. data).

Table 2. Breakdown coefficients (k ; $d^{-1} \pm$ standard deviation) for Picea mariana needle strings in Southern Indian Lake.

Shoreline	Interval (d)		
	0-41	328-384	0-384
Bedrock			
high exposure	0.0051 ± 0.0014	0.0076 ± 0.0043	0.0097 ± 0.0002
low exposure	0.0067 ± 0.0012	0.0080 ± 0.0072^a	0.0041 ± 0.0004
Clay			
high exposure	0.0051 ± 0.0013	0.0037 ± 0.0019	0.0019 ± 0.0001
low exposure			
3 mm-mesh	0.0054 ± 0.0012	0.0329 ± 0.0072	0.0070 ± 0.0005
50 μ m-mesh	0.0054 ± 0.0014	0.0033 ± 0.0006	0.0011 ± 0.0001
Mean	0.0055	-	0.0057^b

^a Calculated for 335-384 d.

^b Clay low exposure, 50 μ m-mesh not included in mean.

Table 3. Numbers and taxa of larval Chironomidae, within Picea mariana needle packs in Southern Indian Lake, ingesting needle tissue during the 328-384 d colonization periods.

Taxon	Number of larvae			
	Shoreline			
	Clay low exposure	Clay high exposure	Bedrock low exposure	Bedrock high exposure
Orthoclaadiinae				
<u>Brillia flavifrons</u>	3	0	0	0
<u>Heterotrissocladius</u> <u>changi</u>	0	0	1	0
Chironominae				
Tanytarsini				
genus 1	0	0	0	2
Chironomini				
<u>Chironomus</u>	1	0	2	9
<u>Glyptotendipes</u>	1	0	0	0
<u>Microtendipes</u>	3	0	0	0
<u>Paratendipes</u>	0	0	1	0
<u>Phaenopsectra</u> <u>punctipes</u>	41 ^a	1	18 ^b	4
<u>Polypedilum</u>	0	1	0	0
Total (total larvae collected)	49(312)	2(229)	22(291)	6(108)
% of total larvae collected	16	1	8	6

^a Includes 12 larvae found within the mesophyll of needles.

^b Includes 8 larvae found within the mesophyll of needles.

Table 4. Analysis of variance (Snedecor and Cochran 1980) on mean numbers of macroinvertebrates per needle string and per gram final needle string dry weight (3 mm-mesh bags) in Southern Indian Lake.

Source of variation	Interval (d)					
	0-41		328-384		0-384	
	# per string	# per gram	# per string	# per gram	# per string	# per gram
shoreline type	n.s.	n.s.	**	n.s.	**	n.s.
wave exposure	*	*	**	**	**	**
interaction: shoreline type x wave exposure	n.s.	n.s.	**	**	**	**

n.s. - not significant ($p > 0.05$).

* - significant only for 34 and 41 d ($p < 0.05$).

** - significant ($p < 0.01$).

Table 5. Mean numbers of larvae per string for taxa of Chironomidae collected from Picea mariana needle strings in Southern Indian Lake during the 0-41 d and 328-384 d colonization periods.

Legend:

Abundance (mean no. per string)	Symbol
0	○
0.1	●
0.1-0.5	●
0.6-1.0	●
1.1-5.0	●
5.1-7.5	●

Continued...

Table 5. Continued.

Taxon	Abundance (mean # per string)							
	Shorelines							
	Clay low exposure		Clay high exposure		Bedrock low exposure		Bedrock high exposure	
	0-41	328-384	0-41	328-384	0-41	328-384	0-41	328-384
Tanypodinae								
<u>Ablabesmyia</u> Joh.	●	●	●	●	●	●	●	●
<u>Procladius</u> Skuse	●	●	●	●	●	●	○	●
<u>Thiennemannimyia</u> (T.) <u>norena</u> (Rob.)	○	○	○	○	○	○	●	○
genusT1	●	●	●	●	●	●	○	○
genusT2	●	●	●	●	●	●	●	○
genusT3	●	●	●	●	○	○	○	○
Orthocladiinae								
<u>Brillia flavifrons</u> (Joh.)	●	●	●	●	●	○	●	●
<u>Corynoneura</u> Wennertz	●	●	●	○	●	○	●	●
<u>Cricotopus</u> van der Wulp	○	●	○	○	●	○	●	●

Continued...

Table 5. Continued.

Taxon	Abundance (mean # per string)							
	Shorelines							
	Clay low exposure		Clay high exposure		Bedrock low exposure		Bedrock high exposure	
	0-41	328-384	0-41	328-384	0-41	328-384	0-41	328-384
<u>Heterotrissocladius changi</u> Saether	○	●	●	●	●	●	●	○
<u>Orthocladius</u> van der Wulp	●	○	○	○	○	●	○	○
<u>Parametriochnemus</u> Goet.	○	○	●	○	○	●	○	○
<u>Psectrocladius</u> Kieffer	●	●	●	○	○	●	○	○
Chironominae								
Chironomini								
<u>Chironomus</u> Meigen	●	●	●	●	●	●	●	○
<u>Cryptochironomus</u> Kieffer	●	○	○	○	●	○	○	○
<u>Dicrotendipes</u> Kieffer	●	●	●	○	●	●	●	○
<u>Endochironomus nigricans</u> (Joh.)	●	○	○	○	○	●	○	○
<u>Glyptotendipes</u> Kieffer	●	●	○	○	●	●	○	●

Continued...

Table 5. Continued.

Taxon	Abundance (mean # per string)							
	Shorelines							
	Clay low exposure		Clay high exposure		Bedrock low exposure		Bedrock high exposure	
	0-41	328-384	0-41	328-384	0-41	328-384	0-41	328-384
<u>Microtendipes</u> Kieffer	●	●	●	●	●	●	●	●
<u>Parachironomus</u> Lenz	●	●	●	●	●	●	●	●
<u>Paratendipes</u> Kieffer	○	○	●	●	○	●	●	○
<u>Phaenopsectra punctipes</u> (Wied.)	●	●	●	●	●	●	●	●
<u>Polypedilum</u> Kieffer	○	○	●	●	●	●	○	○
Tantarsini								
<u>Cladotanytarsus</u> Kieffer	●	●	●	●	●	●	●	●
<u>Paratanytarsus</u> Bause	○	●	○	○	○	○	○	○
<u>Stempellinella</u> Brundin	○	○	○	●	○	○	○	○
genus 1 (prob. <u>Microsectra</u> Kieffer)	●	●	●	●	●	●	●	●

Table 6. Relative abundance (% of identified larvae) of the five most common taxa of larval Chironomidae collected from Picea mariana needle strings in Southern Indian Lake during the 0-41 d, 328-384 d, and 0-384 d colonization periods.

Shoreline	Relative abundance (% of identified larvae)		
	0-41	328-384	0-384
clay low exposure	1. <u>Phaenopsectra punctipes</u> (55)	1. <u>P. punctipes</u> (38)	1. <u>P. punctipes</u> (48)
	2. Tanytarsini genus 1 (10)	2. <u>Microtendipes</u> (11)	2. <u>Microtendipes</u> (8)
	3. <u>Ablabesmyia</u> (9)	3. <u>Psectrocladius</u> (9)	3. <u>Ablabesmyia</u> (8)
	4. <u>Microtendipes</u> (5)	4. <u>Cladotanytarsus</u> (6)	4. Tanytarsini genus 1 (7)
	5. <u>Corynoneura</u> (3) <u>Chironomus</u> (3) <u>Dicrotendipes</u> (3)	5. <u>Ablabesmyia</u> (6)	5. <u>Psectrocladius</u> (5)
clay high exposure	1. <u>Microtendipes</u> (40)	1. <u>Procladius</u> (26)	1. <u>Microtendipes</u> (30)
	2. <u>P. punctipes</u> (16)	2. <u>Microtendipes</u> (17)	2. <u>Procladius</u> (13)
	3. <u>Ablabesmyia</u> (10)	3. <u>Paratendipes</u> (13)	3. <u>P. punctipes</u> (12)
	4. Tanytarsini genus 1 (7)	4. Tanytarsini genus 1 (10)	4. Tanytarsini genus 1 (8)
	5. <u>Polypedilum</u> (5)	5. <u>P. punctipes</u> (7)	5. <u>Ablabesmyia</u> (7)

Continued...

Table 6. Continued.

Shoreline	Relative abundance (% of identified larvae)		
	0-41	328-384	0-384
bedrock low exposure	1. <u>P. punctipes</u> (41)	1. <u>P. punctipes</u> (32)	1. <u>P. punctipes</u> (31)
	2. <u>Ablabesmyia</u> (12)	2. <u>Chironomus</u> (17)	2. <u>Chironomus</u> (13)
	3. Tanytarsini genus 1 (9)	3. <u>Procladius</u> (10)	3. <u>Ablabesmyia</u> (8)
	4. <u>Chironomus</u> (8)	4. <u>Paratendipes</u> (9)	4. Tanytarsini genus 1 (8)
	5. <u>Microtendipes</u> (6)	5. Tanytarsini genus 1 (8)	5. <u>Procladius</u> (7)
		6. <u>Microtendipes</u> (8)	
bedrock high exposure	1. <u>P. punctipes</u> (49)	1. <u>Parachironomus</u> (47)	1. <u>P. punctipes</u> (37)
	2. <u>Corynoneura</u> (11)	2. <u>Cladotanytarsus</u> (13)	2. <u>Parachironomus</u> (19)
	3. <u>Chironomus</u> (9)	3. <u>P. punctipes</u> (10)	3. <u>Corynoneura</u> (10)
	4. <u>Paratendipes</u> (7)	4. <u>Corynoneura</u> (9)	4. <u>Chironomus</u> (6)
	5. <u>Parachironomus</u> (6)	5. <u>Cricotopus</u> (7)	5. <u>Cricotopus</u> (5)
			<u>Paratendipes</u> (5)

Table 7. Characterization of Chironomidae communities colonizing *Picea mariana* needle strings in Southern Indian Lake during the 0-41 d, 328-384 d, and 0-384 d colonization periods. [Shannon-Weaver diversity index = H' . Probability that two individuals belong to the same genus (Simpson's diversity index) = C .]

	No. taxa present			H'			C		
	Colonization period (d)			Colonization period (d)			Colonization period (d)		
	0-41	328-384	0-384	0-41	328-384	0-384	0-41	328-384	0-384
clay low exposure	18	19	22	1.751	2.158	2.049	0.328	0.179	0.251
clay high exposure	19	16	20	2.190	2.231	2.402	0.199	0.132	0.139
bedrock low exposure	18	19	23	2.067	2.404	2.379	0.203	0.114	0.142
bedrock high exposure	15	11	17	1.806	1.679	2.038	0.267	0.255	0.192

Table 8. Similarity (no. of taxa in common, Kendall's "Tau", p-value) of Chironomidae communities colonizing Picea mariana needle strings in Southern Indian Lake during the 0-41 d colonization period.

	Bedrock high exposure	Bedrock low exposure	Clay high exposure
Clay low exposure	Not similar (11, 0.203, 0.116)	Similar (14, 0.563, <0.001)	Similar (15, 0.420, 0.005)
Clay high exposure	Not similar (13, 0.088, 0.311)	Similar (15, 0.385, 0.009)	
Bedrock low exposure	Not similar (13, 0.102, 0.287)		

Table 9. Similarity (no. of taxa in common, Kendall's "Tau", p-value) of Chironomidae communities colonizing Picea mariana needle strings in Southern Indian Lake during the 328-384 d colonization period.

	Bedrock high exposure	Bedrock low exposure	Clay high exposure
Clay low exposure	Not similar (11, 0.314, 0.045)	Not similar (14, 0.206, 0.096)	Not similar (13, 0.294, 0.037)
Clay high exposure	Not similar (8, 0.013, 0.456)	Similar (13, 0.486, 0.001)	
Bedrock low exposure	Not similar (8, 0.010, 0.464)		

Table 10. Estimated input of C, N, and P to Southern Indian Lake from the breakdown of inundated *Picea mariana* needles during the first year after impoundment (see text for details of calculation).

Element	Estimated potential input (I_p)		Estimated actual input (I_A)	
	tonnes	g m^{-2} lake surface	tonnes	g m^{-2} lake surface
C	228,800	95	200,000	83
N	2,850	1.19	2,490	1.04
P	337	0.14	295	0.12

Table 11. Breakdown coefficients (k) for needles of various conifer species.

Species	Season or temperature	Duration of study (days)	k (day ⁻¹)	Experimental conditions	Reference
<u>Picea mariana</u>	summer-fall	41	0.0055	impounded lake	this study
<u>Picea mariana</u>	summer-summer	384	0.0019-0.0097	impounded lake	this study
<u>Picea sp.</u>	not given	42	0.005 ^a	laboratory	Ostrofsky (1978)
<u>Picea sp.</u>	not given	70	0.002 ^a	laboratory	Ostrofsky (1978)
<u>Abies amabilis</u>	year-round	732	0.003-0.0037 ^a	subalpine lake	Rau (1978)
<u>Pinus contorta</u>	5-6°C (mean)	521	0.006	pond	Hodkinson (1975a)
<u>Pinus ponderosa</u>	fall-spring	168	0.0038	stream	Short et al. (1980)
<u>Pinus resinosa</u>	fall-spring	285	0.0030	stream	Bärlocher et al. (1978a)
<u>Pseudotsuga menziesii</u>	2-18°C	240	0.0018-0.0100	stream	Triska and Buckley (1978)
<u>Tsuga mertensiana</u>	year-round	732	0.0001-0.0016 ^a	subalpine lake	Rau (1978)
mixture of <u>Pseudotsuga menziesii</u> and <u>Tsuga heterophylla</u>	8°C (mean)	100	0.0057	stream	Sedell et al. (1975).
mixture of <u>Pseudotsuga menziesii</u> and <u>Tsuga heterophylla</u>	8°C (mean)	202	0.0025-0.0131	stream	Sedell et al. (1975)

^a Estimated from available data in the publication.

Figure 1. Location of Southern Indian Lake.

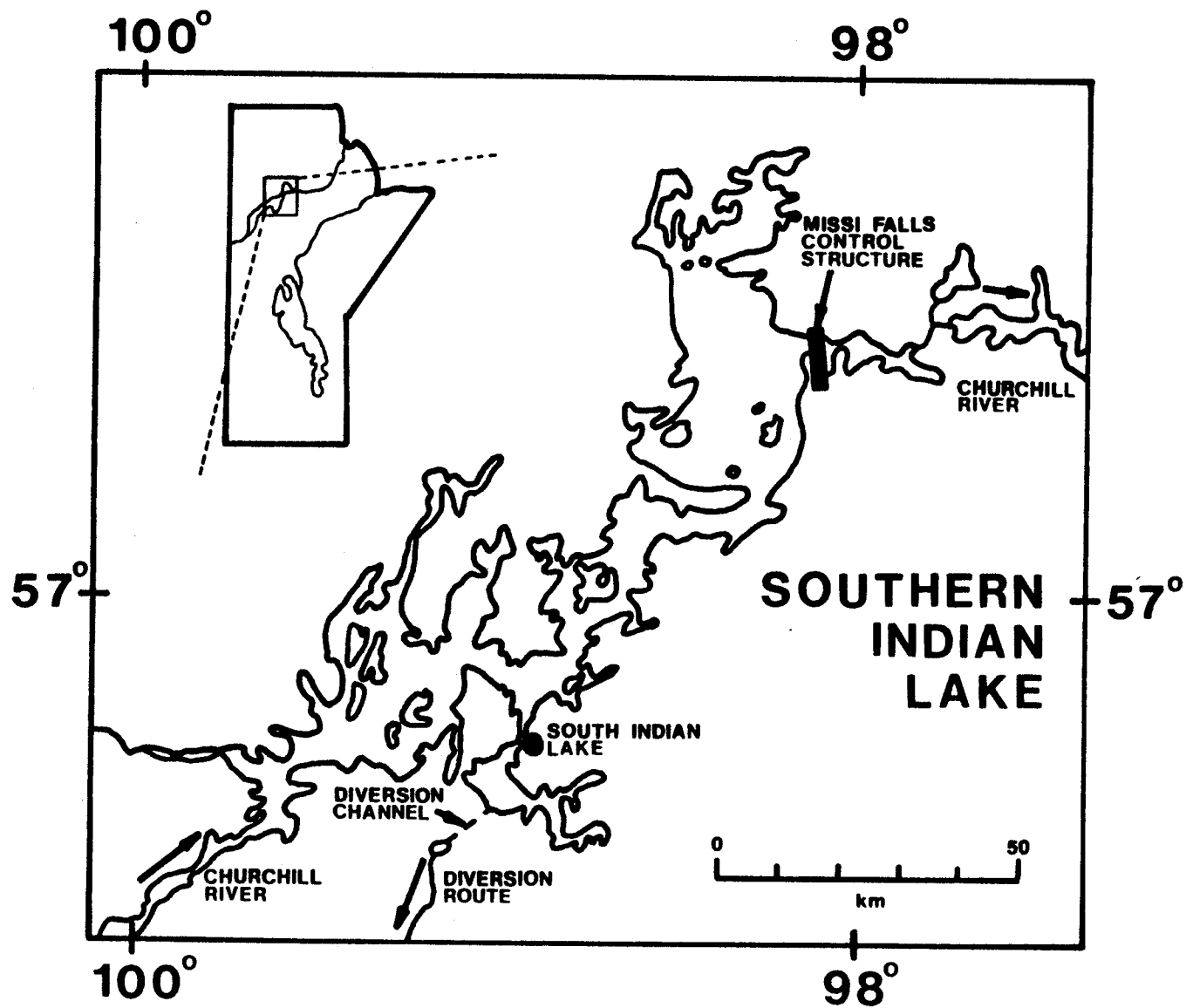


Figure 2. Picea mariana experimental needle packs (3 mm-mesh pack on bottom and 50 μ m-mesh pack on top.



Figure 3. Breakdown of Picea mariana needle strings in Southern Indian Lake during the 0-41 d and 328-384 d colonization periods.

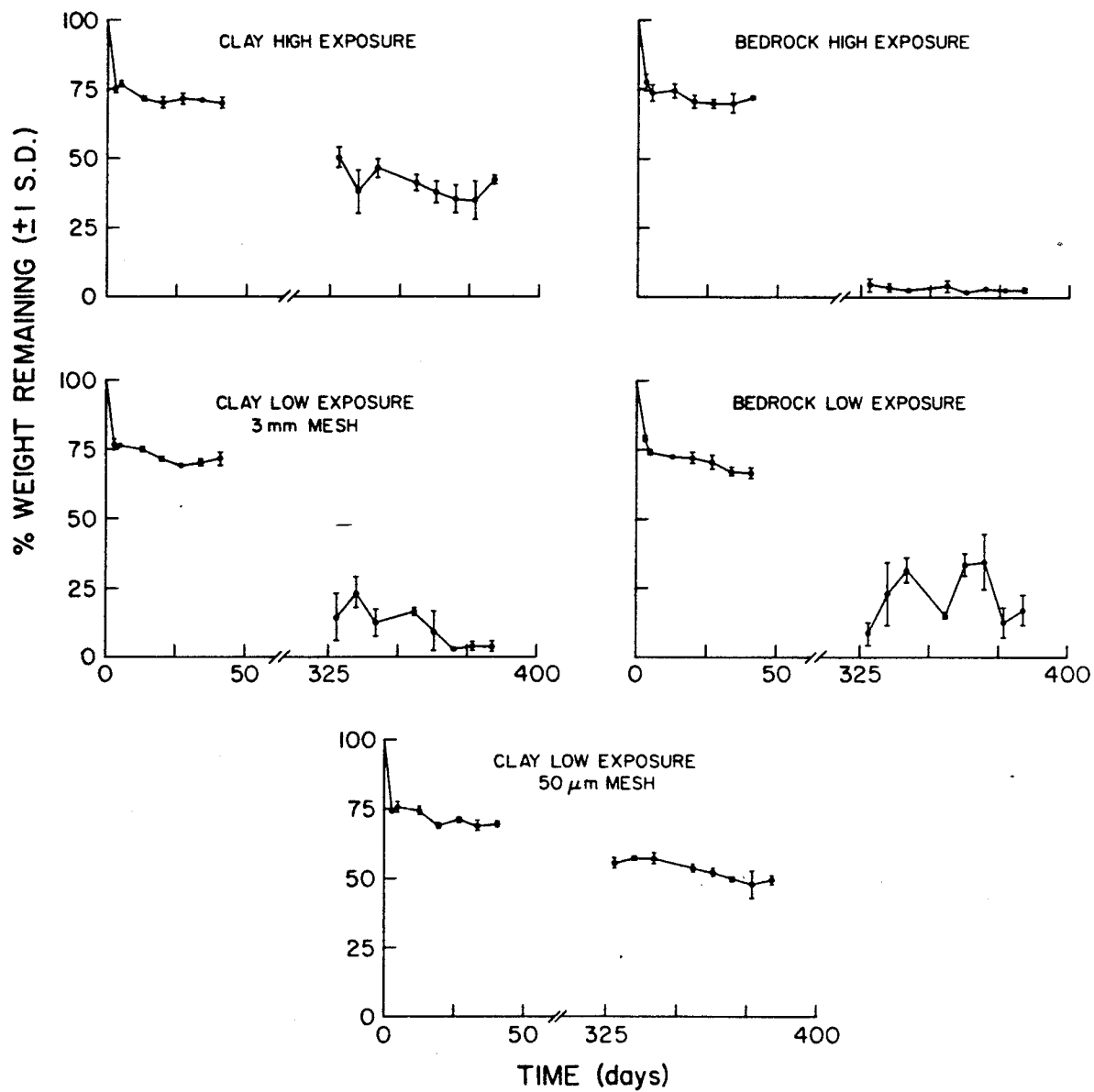
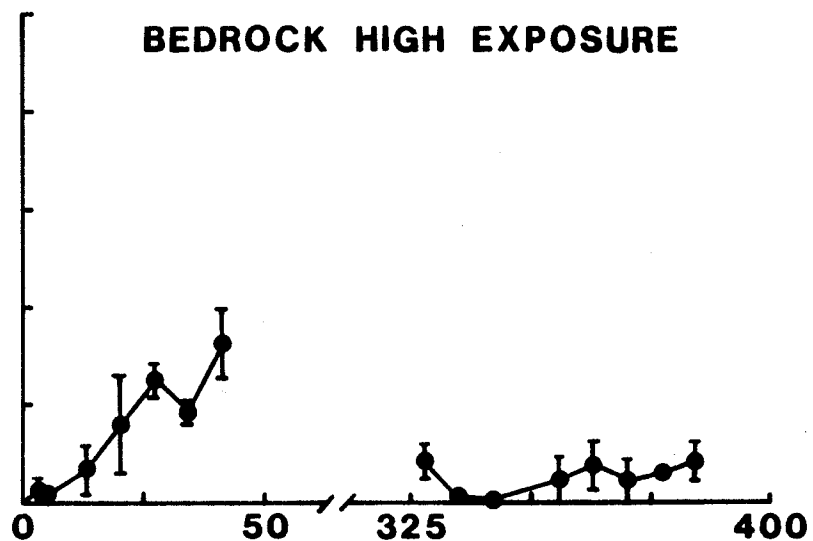
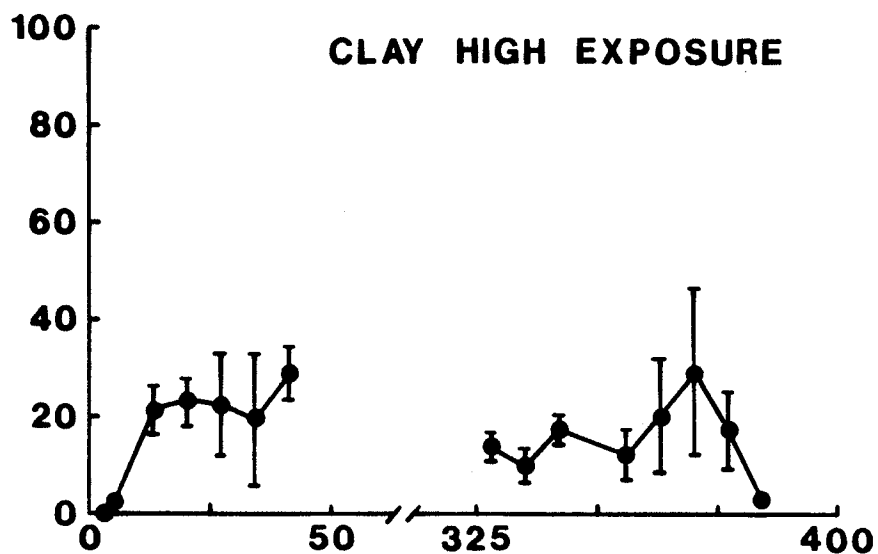
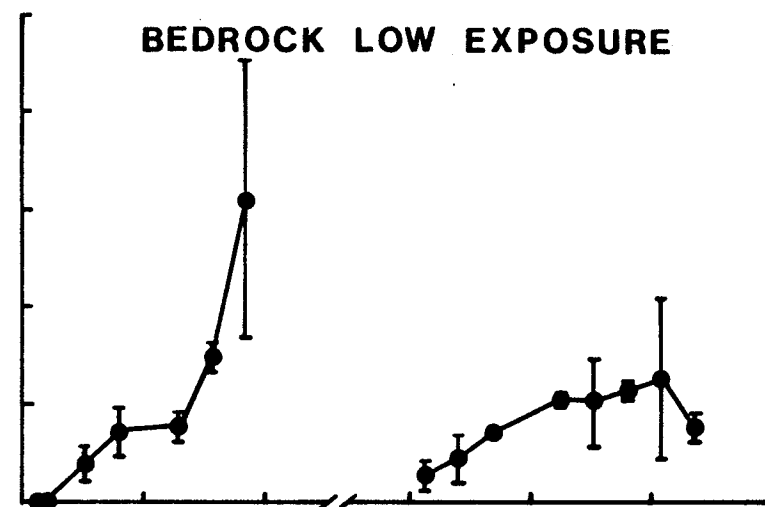
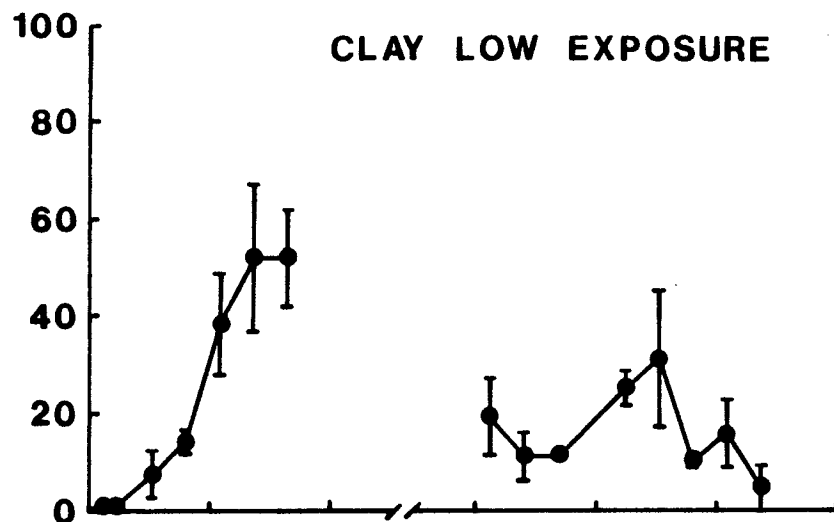
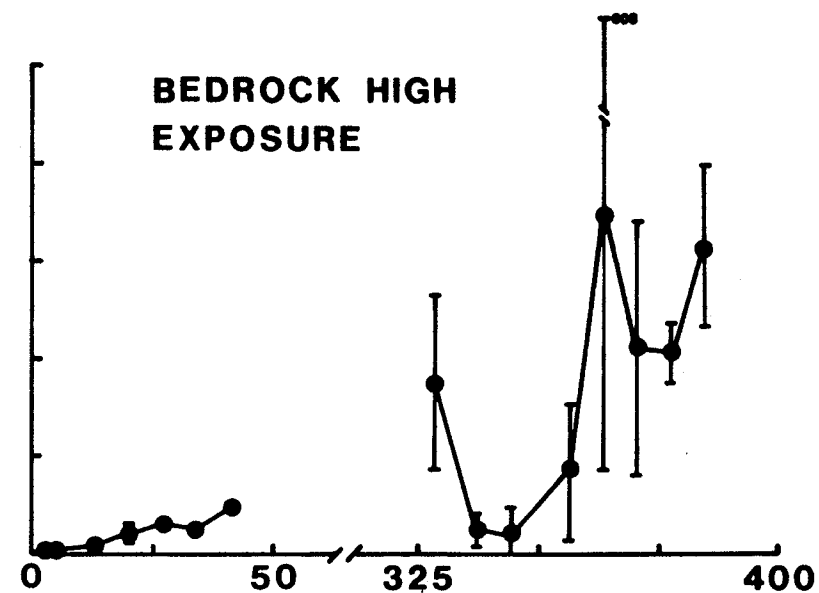
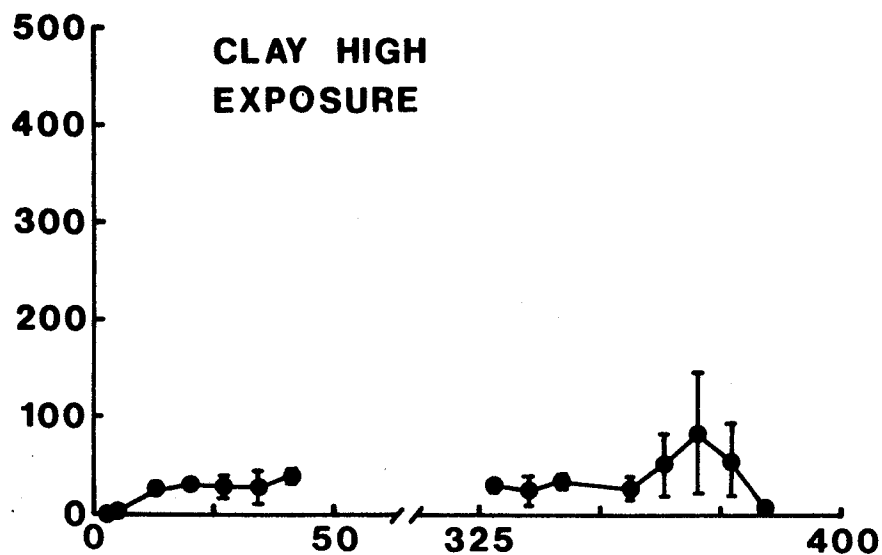
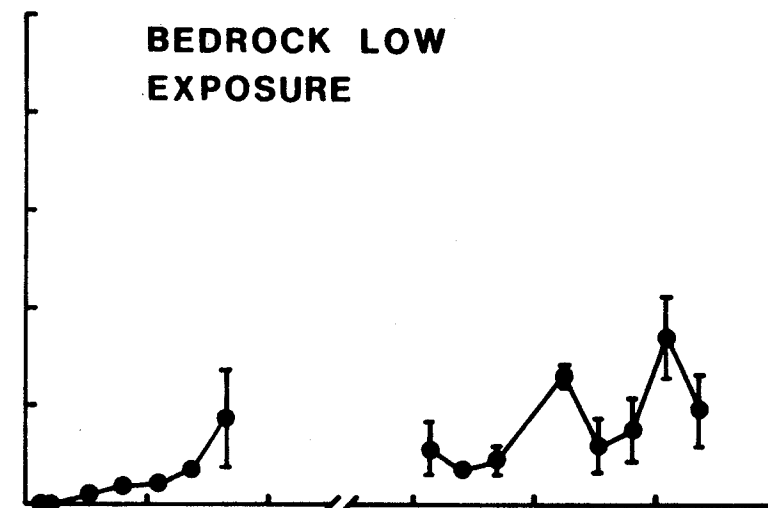
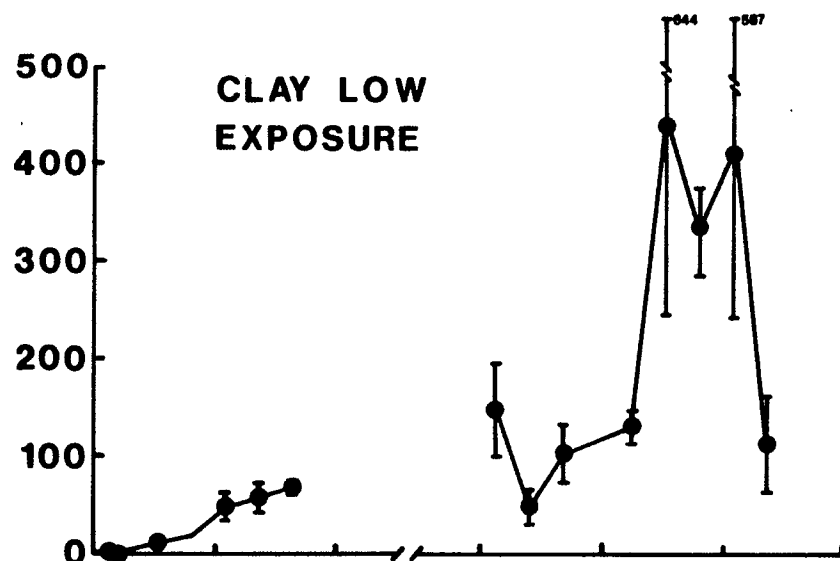


Figure 4. Mean number of macroinvertebrates per string colonizing Picea mariana needle strings in Southern Indian Lake during the 0-41 d and 328-384 d colonization periods.

MEAN NO. PER STRING (\pm SD)

TIME (days)

Figure 5. Mean number of macroinvertebrates per gram final needle string dry weight colonizing Picea mariana needle strings in Southern Indian Lake during the 0-41 d and 328-384 d colonization periods.

MEAN NO. PER GRAM (\pm SD)

TIME (days)

Figure 6. Placement of the benthic and suspended Picea mariana needle packs at the clay low exposure shoreline in Southern Indian Lake.

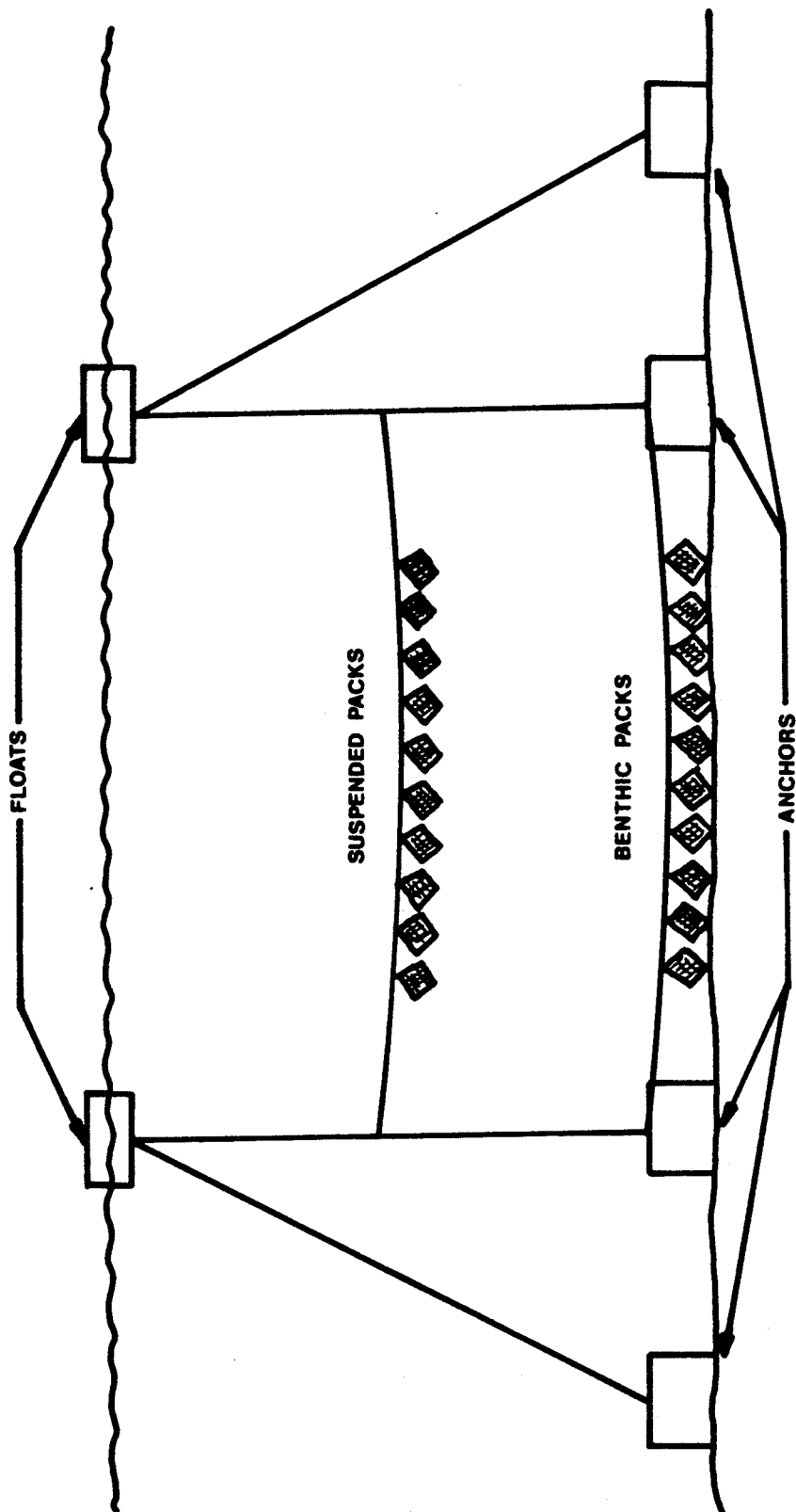


Figure 7. Mean numbers of Chironomidae colonizing Picea mariana needle strings in Southern Indian Lake during the 0-41 d and 328-384 d colonization periods.

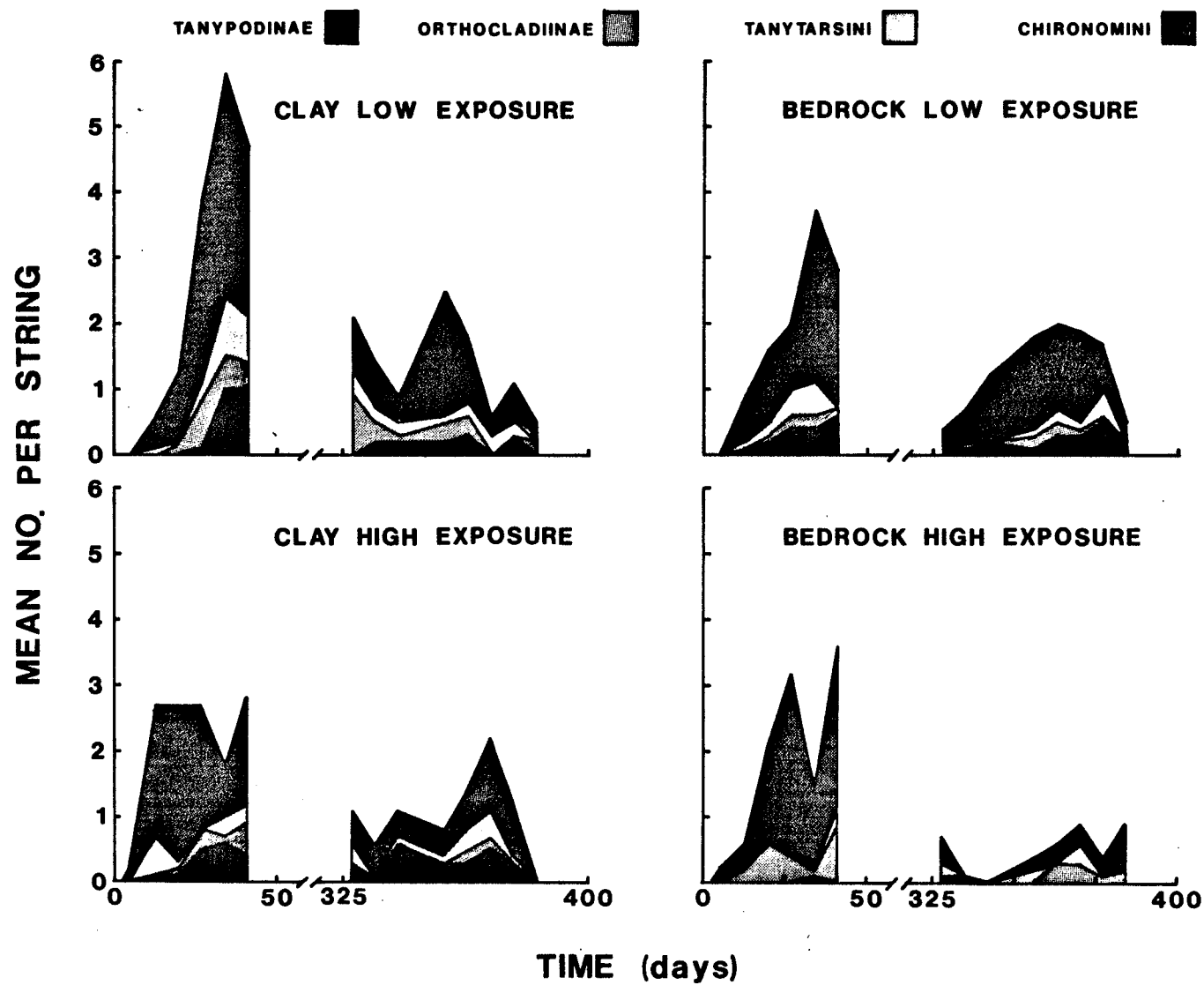


Figure 8. Mean numbers of macroinvertebrates colonizing empty 3 mm-mesh bags; benthic and suspended Picea mariana needle packs; and packs containing fresh Picea mariana needles in Southern Indian Lake.

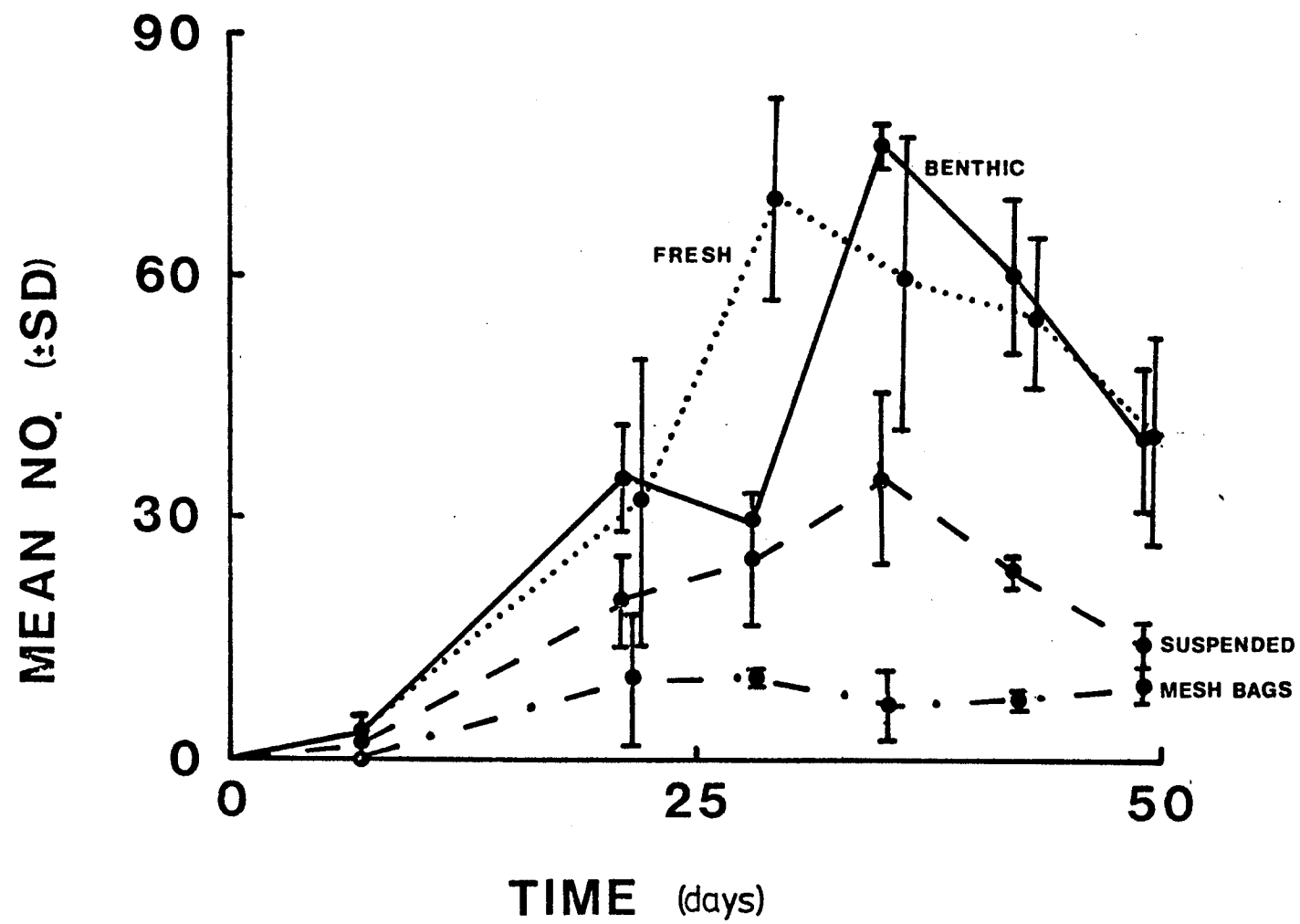


Figure 9. Partitioning of weight losses from Picea mariana needle strings in Southern Indian Lake during 0-41 d and 328-384 d colonization periods. A = all shorelines (0-3 d), $\log_e (\%R) = \log_e (100.00) - 0.0907t$; B = leaching, assumed to be 25% of initial dry weight; C = all shorelines (3-41 d), $\log_e (\%R) = \log_e (75.86) - 0.0025t$; D = clay low exposure 50 μm exclusion packs (328-384 d), $\log_e (\%R) = \log_e (172.42) - 0.0033t$; E = clay low exposure 3 mm-mesh packs (328-384 d), $\log_e (\%R) = \log_e (927335.52) - 0.0329t$; F = clay high exposure shoreline (328-384 d), $\log_e (\%E) = \log_e (150.96) - 0.0037t$; G = bedrock low exposure shoreline (328-384 d), $\log_e (\%R) = \log_e (370.98) - 0.0080t$; H = bedrock high exposure shoreline (328-384 d), $\log_e (\%R) = \log_e (41.56) - 0.0076t$.

