The importance of beaver lodges in structuring littoral communities in boreal headwater lakes

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Abstract: The littoral zones of many boreal headwater lakes in northwestern Ontario are composed of rocks, boulders, and sand, with sparse macrophyte growth. This study investigated the possibility that abandoned beaver lodges might structure littoral communities in these systems through providing accumulations of coarse woody debris and entrapped sediment. The richness and abundance of 10 benthic macroinvertebrate taxa, 6 species of small fishes, and 2 species of amphibians were found to be significantly elevated near beaver lodges compared with areas of sand and rocks otherwise characteristic of the littoral zones in these lakes. Beaver in Ontario are generally regarded as a nuisance or a resource; wildlife managers therefore encourage extensive trapping before large populations can become established. The results of this study suggest that beaver provide an important habitat resource for littoral communities in boreal headwater lakes. As a result, endorsement of limiting beaver populations through increased trapping should be reexamined for regions containing macrophyte-impoverished lakes with a rocky shore.

Résumé : Les zones littorales de plusieurs lacs d'amont de la région boréale, dans le nord-ouest de l'Ontario, sont constituées de pierres, de cailloux et de sable et comportent peu de macrophytes. Est examinée dans cette étude la possibilité que les huttes abandonnées de castors structurent les communautés littorales de ces systèmes en assurant l'amoncellement de gros débris de bois auxquels les sédiments restent accrochés. La richesse et l'abondance de 10 taxons de macroinvertébrés benthiques, 6 espèces de petits poissons et 2 espèces d'amphibiens sont particulièrement élevées près des huttes de castors et beaucoup moins dans les zones sablonneuses et rocheuses caractéristiques de ces zones littorales. En Ontario, les castors sont considérés comme nuisibles ou sont traités comme une ressource; le piégeage est de ce fait fortement encouragé pour empêcher que des populations importantes ne réussissent à s'établir. Il semble au contraire que les castors contribuent à l'établissement d'habitats adéquats pour les communautés littorales des lacs d'amont en zone boréale. L'imposition de limites à la destruction des populations de castors par augmentation du piégeage devrait être réexaminée sérieusement dans les régions de lacs à bords rocheux pauvres en macrophytes. [Traduit par la Rédaction]

Introduction

Once thought to be a component of isolated systems (Forbes 1887), the littoral zone is now considered to be an intermediate stage or ecotone in a dynamic continuum involving transport of material from atmospheric or drainage basin sources to profundal sediments or downstream waters (Likens 1984). Few general studies of shoreline wildlife have been undertaken (e.g., Stauffer and Best 1980; Brusynk and Gilbert 1983), and little is known about the role of terrestrial animals in facilitating or modifying the transport of allochthonous material to aquatic environments (Dobrowolski et al. 1993).

Coarse woody debris (CWD) in lakes provides an important habitat for benthic macroinvertebrates and littoral fishes (Clafin 1968; McLachlan 1970; Nilsen and Larimore 1973; Vogele and Rainwater 1975; Moring et al. 1986, 1989). Beaver (*Castor canadensis*) are prominent vectors in the importing of allochthonous organic matter to fresh waters (e.g., Naiman et al. 1984; Johnston and Naiman 1987, 1990). Several investigations have measured the effects of beaver dam impoundments on lotic invertebrate diversity and abundance, largely caused by alterations in water movement (Sprules 1940; Hodkinson 1975; Naiman et al. 1984; McDowell and Naiman 1986; Smith et al. 1991). No previous study has addressed the role of beaver lodges in structuring communities of lentic fauna. The purpose of the present study was to determine the influence of beaver lodges on the abundance and richness of littoral organisms in Canadian Shield lakes.

Tens of thousands of beaver are trapped annually in Ontario; they comprise up to 70% of the total harvest of all wild furs, which represents an industry worth millions of dollars (Novak 1976). Wildlife managers in Ontario refer to a "beaver resource that is grossly under-harvested," so that there is "an over-abundance of colonies," and therefore "encourage trappers to harvest more beaver than they have been taking so far" (Novak 1976). Although the ecological effects of beaver on riparian forests are generally well understood (e.g., Johnston and Naiman 1990), nothing is known of whether they play a significant ecological role in littoral zone ecology through importing wood into boreal lakes. Such information is essential before any endorsement can be made of a culling of beaver, in response to a need perceived by regulating agencies, before the "dangers of overpopulation" (Novak 1976) due to animals "reaching epidemic proportions" (T. Jagros, Vice President of marketing for the North American Fur Auction, cited in Collins 1995) presumably become manifest.

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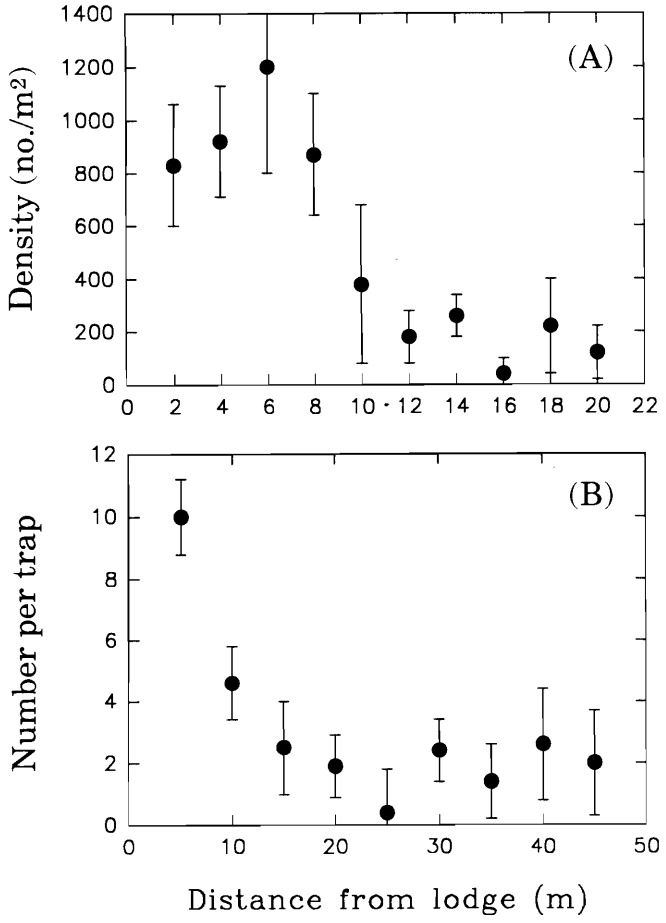
Fig. 1. Attenuation of macroinvertebrate density (mean ± SE) (A) and epibenthos abundance (mean ± SE) (B) with distance from beaver lodges in the study lakes. Six to 14 cores were sampled for distance intervals for macroinvertebrates and 8–18 traps for epibenthos.



Methods

Benthic and epibenthic organisms were sampled within the littoral zones of 4 lakes located 45 km northwest of the town of Atikokan and 150 km southeast of the Experimental Lakes Area in northwestern Ontario (France 1995*a*, 1996; France and Steedman 1996). These are small (26–57 ha) headwater lakes surrounded by dense riparian forest composed of black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). The lakes are ice-covered from November to April, are oligotrophic, and rely upon allochthonous organic matter for part of their metabolic processes (France and Peters 1995; France 1995*b*). Each lake contained 2–7 abandoned beaver lodges at a density of 0.63–1.92 ($\bar{x}$ = 1.14) lodges per kilometre of shoreline. Above-water lodge dimensions were 3–11 m ($\bar{x}$ = 7 m) shoreline length by 3–7 m ($\bar{x}$ = 5 m) backshore width by 1–4 m ($\bar{x}$ = 2 m) height. Lodges extended a further 3–5 m underwater both parallel and perpendicular to the shore. Birch and aspen branches and saplings (5–15 cm diameter) were the major construction material. All lodges surveyed in this study were located along straight shorelines in areas of rock and sand substrate.

Benthic macroinvertebrates were sampled with a 7.62 cm diameter hand-held corer that could be forced into the substratum (France 1990, 1995*c*). All cores were taken within the littoral fringe at wading depths of 0.2–0.5 m, a range that does not affect macroinvertebrate density (France and Stokes 1988). During September 1992, 12 samples were taken from each of 2 sites in 3 habitat types within all 4 study lakes (a total of 288 cores). These habitats were (*i*) the dense mulch of wood fragments ≤3 cm long associated with previous feeding activity by beaver and located 0.5–2.0 m from the lodges, (*ii*) thick organic sediments situated within wave-protected sediment-deposition embayments, and (*iii*) sand accumulations within an overlying layer of flocculent detritus ≤0.3 cm deep found between rocks. During September 1993, 12 samples were taken along transects 1–21 m from each of 2 lodges within all 4 study lakes (a total of 96 cores). The substrate closest to beaver lodges was composed of dense accumulations of CWD generally 2–4 cm long, the substrate farthest away was sand with a covering of detritus <0.3 cm long, and substrates at intermediate distances consisted of a mixture of CWD and sand. In both years, following gentle sieving (200 μm) at the lake site, samples were hand-sorted in the laboratory while the animals were still alive, and identified to order and enumerated within 48 h of collection, as in France (1990, 1995*c*), France and Stokes (1988), and France et al. (1991).

Epibenthic organisms were sampled with modified minnow traps (painted black, with enlarged openings) baited with fish-flavored canned cat food and beef-flavored canned dog food contained in perforated plastic film canisters, as in France (1991, 1993*a*). During September 1992, 36 traps were placed in water 1–3 m deep around the perimeter of each of the study lakes in 3 habitat types (a total of 144 traps): (1) CWD ≤3 m of beaver lodges, (2) accumulations of partially submerged windthrow trees, and (3) bare rocks or boulders. During September 1993, 8–10 traps were set along transects 2–47 m from each of 2–4 lodges within all 4 study lakes (a total of 128 traps). In both years, traps were collected following overnight sets.

Before analysis, data from traps and cores were fourth-root transformed to stabilize variances (Downing 1981; France 1987). Differences in total trap catches and core densities among the 3 habitats (beaver lodges, sand–rock, and windthrow or sediments) sampled in 1992 were analyzed using ANOVA and Duncan's multiple range tests (P = 0.05). Taxon-specific comparisons were made between lodges and sand–rock habitats by combining the 2 years of data. Using the 1993 transect data, average abundances were compared between beaver lodge habitats (i.e., ≤8–10 m proximity) and sand–rock habitats (i.e., >8–10 m distant). The total numbers of such comparisons for all lodges for both years were 16 for macroinvertebrates and 17 for epibenthos. These values were summed to provide an indication of the overall suitability of each of the 2 habitats in terms of organism richness. Taxon-specific differences in trap catches or core densities between the sand–rock and beaver lodge habitats were analyzed with paired t tests (P = 0.05). These values were summed to provide an indication of the overall suitability of each of the 2 habitats in terms of organism abundance.

Results

Animal abundance was elevated in proximity to beaver lodges to distances of about 8–10 m (Fig. 1). Total densities of benthic macroinvertebrates were, on average, almost three times and significantly higher in CWD near lodges than in sand near rocks (Fig. 2A). Likewise, densities of epibenthic organisms (fishes, crayfish, diving beetles, large hemipterans, tadpoles, newts, leeches) were over three times and significantly higher near lodges than above rocks (Fig. 2B). There were no significant differences in abundance of macroinvertebrates between lodges and distant bays where organic sediment had accumulated, nor in the abundance of epibenthos between lodges and distant groupings of windthrow trees.

In 12 cases, a particular macroinvertebrate taxon was

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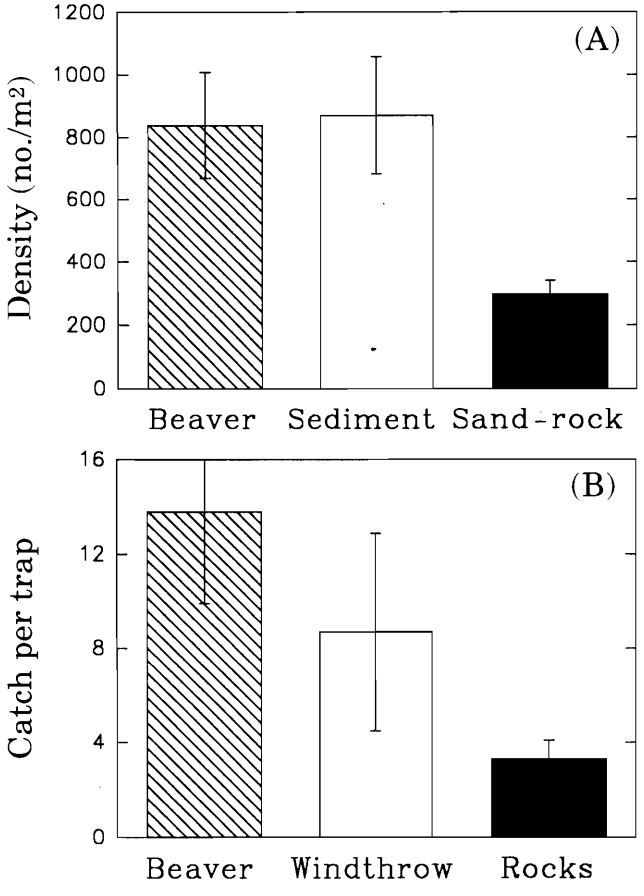
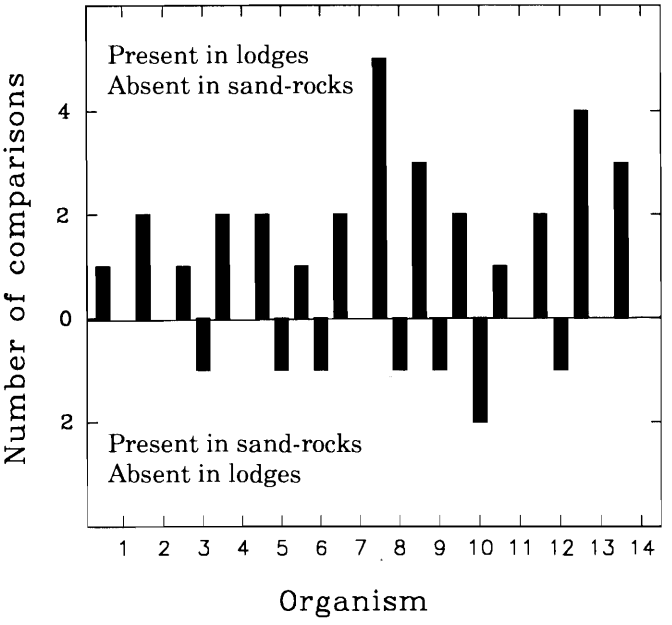
Fig. 2. Comparisons of mean total density (±SE) of benthic macroinvertebrates between the dense mulch of wood fragments (CWD) near beaver lodges, organic sediments in distant bays, and sand between rocks (A) and mean total abundance (±SE) of epibenthic fauna associated with CWD near beaver lodges, distant submerged windthrow trees, and rocks in 4 headwater boreal lakes (B).



found in the beaver lodge habitat and not in the sand–rock habitat, but in only 3 cases did the reverse situation occur (Fig. 3). In 12 cases, a particular fish species was found near beaver lodges and not above rocks, but in only 4 cases did the reverse situation occur. In 6 cases, a particular amphibian species was found near beaver lodges and not above rocks, but in only a single case did the reverse situation occur.

For macroinvertebrates, over three-quarters of the taxon-specific comparisons between lodges and sand–rocks indicated higher densities in the former habitat. Net differences between the number of significantly greater densities in the sand–rock and the lodge habitats subtracted from the reciprocal indicated that amphipods (*Hyalella azteca*), the dominant taxon observed in the littoral zone of these lakes, represented the macroinvertebrate taxon most closely associated with beaver lodges (Fig. 4). Similarly, for epibenthic fauna, almost three-quarters of the taxon-specific comparisons between lodges and rocks indicated higher abundances in the former habitat. Net differences between the number of significantly greater trap abundances above rocks and near lodges subtracted from the reciprocal indicated that northern redbelly and finescale dace (*Phoxinus* spp.), the dominant fishes observed within these littoral zones, represented the

Fig. 3. Taxon-specific comparisons of richness between beaver lodges and sand–rock habitats indicating presence in one habitat and absence in the other. Taxa are as follows: 1, Amphipoda (*Hyalella azteca*); 2, Ephemeroptera; 3, Trichoptera; 4, Diptera; 5, Oligochaeta; 6, Coleoptera; 7, northern redbelly and finescale dace (*Phoxinus* spp.); 8, slimy sculpins (*Cottus cognatus*); 9, brook sticklebacks (*Culea inconstans*); 10, fathead minnows (*Pimephales promelas*); 11, white suckers (*Catostomus commersoni*); 12, tadpoles (*Rana clamitans*); 13, newts (*Notophthalmus viridescens*); 14, large hemipterans.



epibenthic taxon most closely associated with beaver lodges (Fig. 4). Crayfish (*Orconectes virilis*), in contrast, were significantly more abundant above rocks than in CWD.

Discussion

Ecological significance

Organisms living in harsh environments can be distributed extremely nonrandomly. Certain regions provide oases of food and habitat in immense and otherwise unproductive deserts. Although relatively discrete, such regions might have roles that are far more important than is suggested by their physical size alone (e.g., France 1993*b*). Apart from traditional dry deserts, oases are thought to occur within aquatic environments in, for example, the High Arctic (France and Sharp 1993) and deep-sea regions (Turner 1981). Such locations can be referred to as ecosystemic centres of organization (Steedman and Regier 1987) or nodes of diversity (Noss and Harris 1986).

The results of the present study indicate that beaver lodges play a similar role as habitat oases in headwater oligotrophic lakes in boreal regions of the Canadian Shield, where the rocky littoral zone precludes extensive macrophyte growth. In such situations, accumulations of CWD occurring through the activities of beaver serve to influence strongly the distribution of benthic and epibenthic organisms along the otherwise marginally hospitable shoreline consisting of sand and rocks. As a result, both richness and density are elevated in proximity to beaver lodges.

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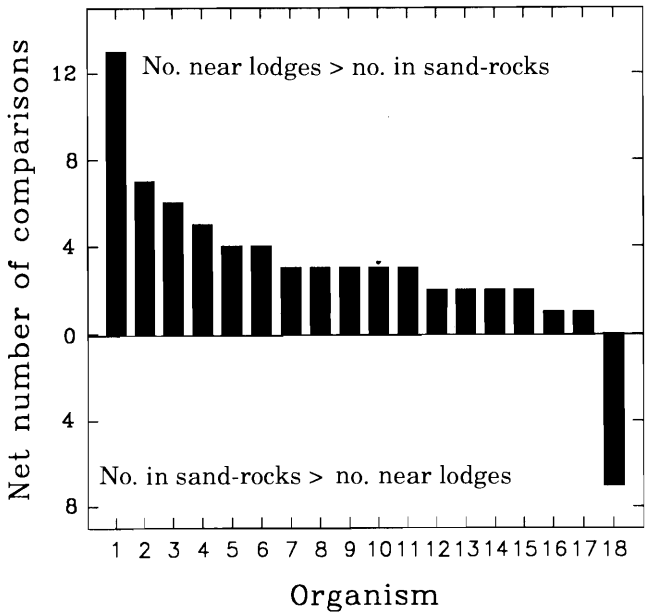
Fig. 4. Taxon-specific comparisons of abundance between beaver lodges and sand–rock habitats indicating the net number of comparisons of significantly higher abundance in one habitat exceeding those of significantly higher abundance in the other. Taxa are as follows: 1, northern redbelly and finescale dace; 2, Amphipoda; 3, sculpins; 4, sticklebacks; 5, pearl dace; 6, newts; 7, large hemipterans; 8, Ephemeroptera; 9, Diptera; 10, Trichoptera; 11, fathead minnows; 12, Coleoptera; 13, large diving beetles; 14, tadpoles; 15, suckers; 16, Hirudinea; 17, Oligochaeta; 18, crayfish (*Orconectes virilis*).



The similarity of macroinvertebrate densities between lodges and distant bays of organic sediment, and in epibenthos densities between lodges and distant groupings of submerged windthrow trees, indicates that there may be nothing particularly unique about beaver lodges themselves apart from their role as centres of large accumulations of CWD and entrapped sediment. Macroinvertebrates are probably attracted to beaver lodges because the accumulated CWD is a food source, a substrate for biofilm growth, an entrapping agent of organic debris and silt, and a refuge from predation (cf. Dudley and Anderson 1982; Eiler 1986). Likewise, littoral fishes are probably attracted to CWD by the elevated concentrations of food there, as well as by the physical structures that can be used for shelter (e.g., Negus 1987; Everett and Ruiz 1993).

Conservation implications

During the 1940s, beaver were almost extirpated from large areas of northwestern Ontario as a result of a bacterial epidemic (Novak 1976). Since that time, transplanting–restocking programs and early restrictions on trapping have led to a marked increase in beaver populations in lakes with shallow muddy bays and a fringe of deciduous riparian trees (Ingle-Sidorowicz 1982). But in the physically less favorable environments of rocky-shored headwater lakes surrounded by predominantly coniferous trees, beaver populations remain at low levels (Novak 1976; personal communication (various trappers interviewed in northwestern Ontario), 1993), despite the recent decrease in the market value of their pelts and a subsequent relaxation of trapping pressure. It is in precisely these boreal headwater lakes, in which vascular macrophytes are rare, that beaver lodges may be most important for structuring littoral communities. In this study, data on lodge frequency and the distribution and abundance patterns of littoral organisms suggest that as much as 10% of the total littoral standing crop of macroinvertebrates, 15% of the total standing crop of littoral fishes, and almost 100% of the standing crop of large diving beetles, hemipterans, and newts are associated with beaver lodges in the study lakes. In rocky-shored boreal headwater lakes that do not have extensive deposition embayments and (or) significant accumulations of windthrow trees, beaver lodges might be even more important.

Although often regarded as either pests (e.g., Ingle-Sidorowicz 1982; Hacker and Coblentz 1993; Lizarralde 1993; see Collins 1995) or fur producers (Novak 1976), beaver are a valuable habitat resource for littoral communities in headwater Canadian Shield lakes through their role as importers of allochthonous material across ecotonal boundaries. As a result, the regulating agencies' enthusiastic endorsement of an expansion of trapping (e.g., Novak 1976; T. Jagros, cited in Collins 1995) should be reexamined for particular regions of the Canadian Shield that comprise predominantly rocky-shored headwater lakes where beaver play an important ecological role in structuring the littoral communities located there.

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