The influence of benthic tundra pond vegetation and prey behavior on zooplankton predation by the flatworm *Mesostoma lingua*

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Experiments were conducted at the Smoking Hills and Tuktoyaktuk, N.W.T., to determine if *Mesostoma lingua*, a common pond inhabitant, preys selectively on co-occurring zooplankton, and whether predation rates are affected by the presence of pond vegetation. Experiments were conducted in 250-mL containers at the sites. *Mesostoma* fed heavily on *Daphnia pulex* and *Chironomus riparius*, but not on *Branchinecta paludosa* or *Diaptomus arcticus*. The presence of alternative prey led to significant reductions in *Daphnia* predation rates, while the presence of the pond plants *Cladophora insignis* and *Drepanocladus aduncus*, which provide shelter and cover, significantly increased predation rates. The advantage of the moss and algal habitat was largely to the predator.

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Des expériences dans les monts Smoking Hills et à Tuktoyaktuk, dans les Territoires du Nord-Ouest, ont servi à vérifier si *Mesostoma lingua*, un organisme assez commun des étangs, exerce une pression sélective sur le zooplancton et si l'efficacité de la prédation est affectée par la présence de végétation. Les expériences ont été faites en nature, dans des contenants de 250 mL. *Mesostoma* se nourrit avidement de *Daphnia pulex* et de *Chironomus riparius*, mais pas de *Branchinecta paludosa* ou de *Diaptomus arcticus*. La présence d'autres proies réduit significativement les taux de prédation de *Daphnia*, mais la présence des plantes d'étangs *Cladophora insignis* et *Drepanocladus aduncus*, qui fournissent abri et couverture, augmente significativement les taux de prédation. La présence de mousses et d'algues avantage le prédateur beaucoup plus que les proies.

[Traduit par le journal]

Introduction

The impact of predation on freshwater zooplankton communities has received considerable attention since the "size–efficiency" hypothesis was first proposed by Brooks and Dodson (1965). They suggested that small-bodied zooplankton species prevail in systems dominated by piscine predators. In contrast, lakes and ponds too shallow to support fish populations are often dominated by invertebrate predators and large-bodied zooplankton. Many studies have documented the importance of invertebrate predators in alpine (Sprules 1972; Dodson 1974; Neill and Peacock 1980; Maly *et al.* 1980; Neill 1984) and arctic ponds (Dodson 1975; Hebert and Loaring 1980; Dodson 1984), although attention in these studies has been focused primarily on predation by members of the Calanoida, Cyclopoida, and Insecta. Few studies (Mead 1978; Maly *et al.* 1980; Schwartz and Hebert 1982) have attempted to assess predation intensity by the neorhabdocoel flatworm *Mesostoma* on pond zooplankton communities. Similarly, the importance of prey refuges in affecting flatworm predation has received little attention, even though most studies (Reynoldson and Young 1963; Young 1973, 1978; Herrmann 1984) have provided some form of refuge for prey. Those studies that have attempted to assess the importance of prey refuges have yielded conflicting results. For example, Pickavance (1971) found that the presence of cover for prey had little effect on the capture efficiency of the planarian *Dugesia tigrina*. In contrast, De Silva (1976) observed higher predation rates by *Dendrocoelum lacteum* in experiments with prey cover. Adams (1980) found that the effect of cover was species dependent: when shelter was provided, *Bdellocephala cephalata* predation on *Asellus* increased, but predation on *Chironomus* decreased.

Mesostoma lingua is a common inhabitant of arctic ponds. In 1984, numerous individuals were commonly observed crawling along the bottom substrate and attached to submerged vegetation in ponds near the Smoking Hills and Tuktoyaktuk,

N.W.T. These same ponds were also notably high in zooplankton production (H. J. MacIsaac and T. C. Hutchinson, personal observations) and were devoid of fish. General descriptions of the zooplankton and algal communities are given in Havas and Hutchinson (1983) and in Sheath *et al.* (1982). In this study we attempt to determine whether *M. lingua* feeds selectively on pond zooplankton, and whether predation rates are affected by the presence of benthic vegetation, a potential prey refuge.

Materials and methods

Flatworms (*Mesostoma lingua* Abildgaard), fairy shrimp (*Branchinecta paludosa* Muller), water fleas (*Daphnia pulex* Leydig), copepods (*Diaptomus arcticus* Marsh), and midge larvae (*Chironomus riparius* Townes) were collected by pulling a fine-meshed dip net through the near-shore waters of a large (26 000 m²; Havas 1980), shallow (1 m) tundra pond at Cape Bathurst, N.W.T., near the Smoking Hills. *Chironomus riparius* were also collected from a pond near Tuktoyaktuk, N.W.T. All collections were made between 23 July and 1 August 1984. The Cape Bathurst pond appeared to be a submerged tundra polygon and was bordered by *Dryas integrifolia* dominated vegetation, with *Arctophila fulva* growing into the shallow water. Profuse blooms of algae (*Cladophora insignis*) interspersed with benthic moss (*Drepanocladus aduncus*) were common throughout the pond, growing on dead *Salix repens*. Test animals were kept for a maximum of 1 day prior to testing, except *Mesostoma*, which were starved for a period of 24 h. Test temperatures ranged between 5 and 12°C, which were natural air temperatures at the sites. Experimental pond water had a pH greater than 8.0, and experiments were conducted under conditions of 24-h continuous light.

To determine predator selectivity, *D. pulex*, *D. arcticus*, and *B. paludosa* were offered alone, and in all combinations, to *Mesostoma*. Experiments consisted of randomly placing 20 adult prey and 10 mature predators into plastic beakers containing 250 mL pond water. Although the predator to prey ratio may appear high, it seems to occur in the natural microenvironment of near-shore algal beds, where high densities of many species congregate. Two repeat experiments per
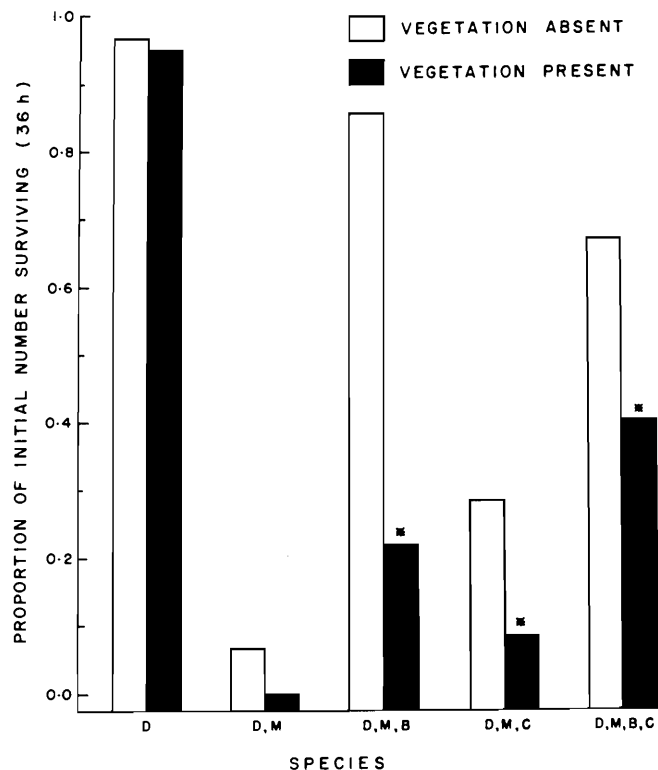
FIG. 1. Effects of other species and pond vegetation on survival of *Daphnia pulex*. Species code: D, *Daphnia pulex*; M, *Mesostoma lingua*; B, *Branchinecta paludosa*; C, *Diaptomus arcticus*. Asterisks (*) indicate a significant difference ($p < 0.01$) between treatments with and without vegetation.

FIG. 2. Effects of other species and pond vegetation on survival of *Branchinecta paludosa*.

feeding treatment were conducted in the field at the Smoking Hills, while a third replicate was performed in the laboratory at Tuktoyaktuk. Because of difficulties encountered in collecting large numbers of chironomids in early August, predator selectivity tests involving the other co-occurring species were not attempted. Additionally, all test parameters (e.g., test volume, predator and prey numbers, and algal and moss weights) were halved for chironomid experiments, and only two replicates per feeding treatment were conducted. The duration of all experiments was 36 h, after which survivors of both predators and prey were enumerated.

To determine whether predation rates are affected by the presence of benthic vegetation, approximately 0.64 g of the filamentous alga *Cladophora insignis* and 0.17 g of the moss *Drepanocladus aduncus* (dry weights) were collected from the same pond as the zooplankton and were added to a series of test containers. Prior to use, the algae and moss were hand cleaned to remove zooplankton, chironomids, flatworms, and debris. Variability between replicates was generally low; hence, there was no apparent test-location effect. Data for replicates were pooled prior to analysis using the SAS procedure Funcat (Statistical Analysis System Institute 1982). Funcat analysis was employed to evaluate overall "species" and vegetation effects on the survival of a species, while χ^2 tests were used to test for individual species or vegetation effects.

Results

Mesostoma preyed on *Daphnia* very actively, while the introduction of additional prey species reduced the rate of *Daphnia* predation (Fig. 1). For example, *Daphnia* survivorship was significantly affected by the presence of other species ($p < 0.01$) and pond vegetation ($p < 0.01$). *Daphnia* survivorship differed significantly ($p < 0.05$ or less) from controls in all trials in which *Mesostoma* were present (Fig. 1). This was most pronounced in feeding trials in which *Daphnia*
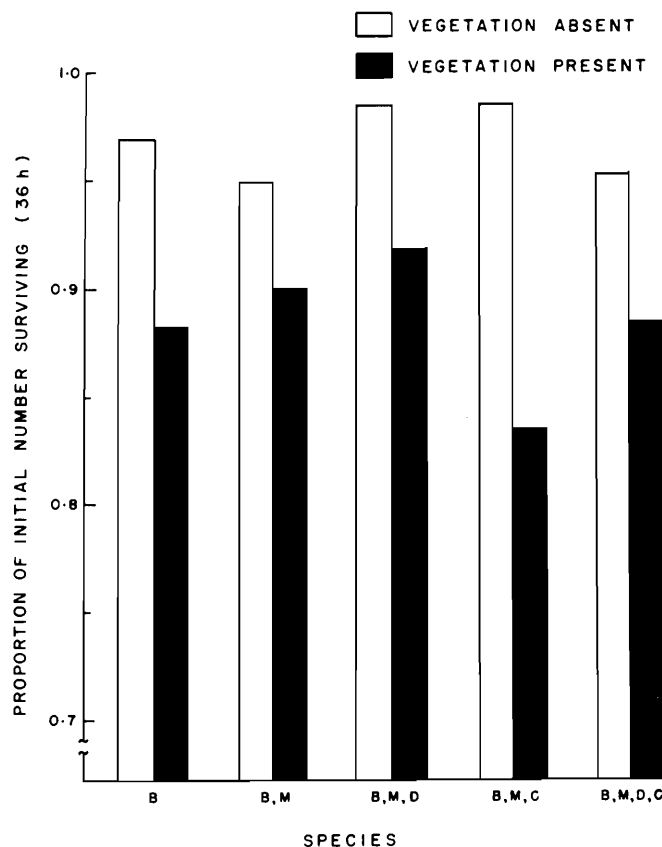
was the only prey species offered. *Daphnia* survivorship was low (6.6%) in containers with *Mesostoma* but without algae and moss, and nonexistent in those with pond vegetation. *Mesostoma* were observed to produce greater amounts of mucus in containers lacking vegetation than in treatments with algae and moss.

Daphnia mortality was significantly ($p < 0.05$ or less) lower in *Mesostoma* feeding experiments in which an alternative prey species (either fairy shrimp or copepods) was present than when it was offered alone. This trend was observed in trials across vegetation treatments, although *Daphnia* survival was significantly ($p < 0.01$) higher in containers without vegetation (Fig. 1). Additionally, the presence of fairy shrimp reduced predation of *Daphnia* more than did that of copepods, both with and without pond vegetation ($p < 0.05$ and $p < 0.01$, respectively). It is of interest that the reduction in water flea predation observed when other potential prey were available to the *Mesostoma* was not accompanied by predation on these other species. Hence the predator was not merely switching from one prey type to another, but rather was far less successful in capturing any prey. The presence of *Branchinecta* especially seemed to disproportionately enhance *Daphnia* survival.

The lowest observed levels of predation on *Daphnia*, for any treatments in which vegetation was provided, occurred when both fairy shrimp and copepods were present (Fig. 1). In containers with both fairy shrimp and copepods, but without algae and moss, predation on *Daphnia* was less severe than when only copepods were present with them, but was more severe than when fairy shrimp were the only other alternative prey. Again, the presence of moss and algae led to a significant
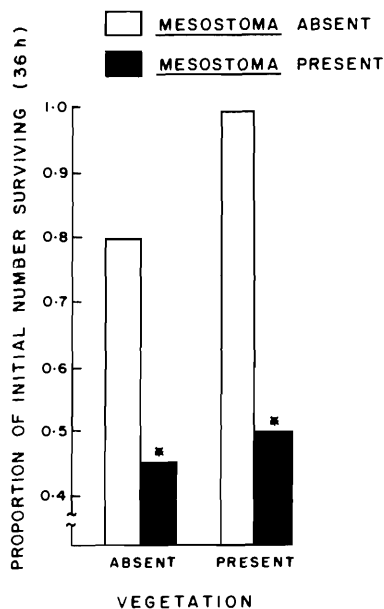
FIG. 3. Effects of *Mesostoma lingua* and pond vegetation on survival of *Chironomus riparius*. Asterisks (*) indicate a significant difference ($p < 0.01$) between treatments with and without *Mesostoma*.

FIG. 4. Effects of the presence of potential prey and pond vegetation on survival of *Mesostoma lingua*.

($p < 0.01$) reduction in *Daphnia* survivorship in experiments with both fairy shrimp and copepods as available prey. It should be noted, however, that *Daphnia* survival in controls with and without pond vegetation did not differ significantly ($p > 0.05$) from one another. Hence, differences in *Daphnia* survival in the aforementioned experiments must be attributed not only to the voracity of *Mesostoma* as a predator, but also to its successful use of algal and moss habitat to enhance its success as a *Daphnia* predator.

The presence of *Mesostoma* had no significant ($p > 0.05$) effect on either fairy shrimp or copepod survivorship. In cases where *Mesostoma* were observed to colonize *Branchinecta*, violent movements by the fairy shrimp repelled and possibly seriously injured the predator. The survival of both fairy shrimp and copepods was high in treatments with and without algae and moss. However, fairy shrimp mortality was significantly ($p < 0.01$) higher overall for treatments with pond vegetation than for treatments without it (Fig. 2). Pond vegetation had no influence on either copepod or chironomid (Fig. 3) survival. Chironomid survival was, however, significantly ($p < 0.01$) decreased by *Mesostoma* in containers both with and without vegetation (Fig. 3).

The presence of algae and moss in test containers led to a significant ($p < 0.01$) increase in the survival of *Mesostoma*, though only in experiments that involved fairy shrimp as a potential prey species (Fig. 4). Thus, not only did *Mesostoma* benefit from increased predation on *Daphnia* and *Chironomus* while living in the algae and moss, but it also was less likely to be wounded in encounters with *Branchinecta*.

Discussion

The results of this study indicate that the presence of pond vegetation may significantly increase the predation success of *M. lingua*. The finding that *M. lingua* is a rapacious predator on *Daphnia* concurs with that of Schwartz and Hebert (1982), who used *Mesostoma ehrenbergii*, *D. pulex*, and *D. laevis* from ponds in southern Ontario, and Maly *et al.* (1980), who
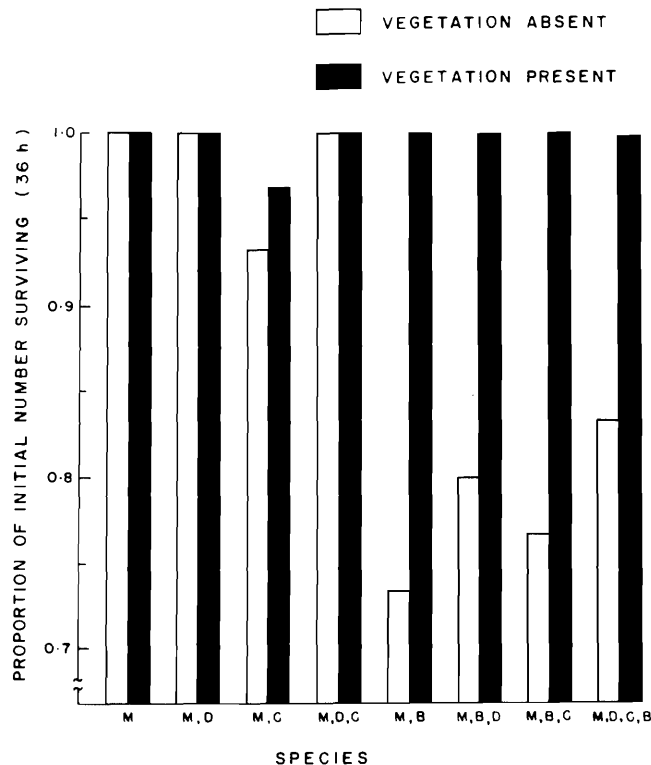
used *M. ehrenbergii* and *D. middendorffiana* from high-altitude ponds in Colorado. It is of special interest that independent investigations from three widely separated locations have yielded similar results.

Schwartz and Hebert (1982) observed that *M. ehrenbergii* preyed selectively on organisms about 1.2 mm in length, with prey up to 2 mm also suffering high mortality. Maly *et al.* (1980) found that *M. ehrenbergii* did not prey on either *Diaptomus shoshone* or *D. coloradensis*, even though the latter species lies within the preferred size range found in Schwartz and Hebert's study. Anderson (1970) observed groups of *Mesostoma* feeding on damaged or dying *D. arcticus*. In the present study, *M. lingua* selectively preyed on *D. pulex* when alternate prey (*D. arcticus* and *B. paludosa*) were available, even though the diaptomids are calorically more favorable than the daphnids (Comita and Schindler 1963). These findings cannot be attributed to size-selective predation alone, as *Daphnia* and *Diaptomus* are approximately the same size. A more feasible explanation involves prey escape mechanisms: copepods are powerful swimmers capable of rapid hops when disturbed by a predator (Zaret 1980). Similarly, fairy shrimp escape from *Mesostoma* and other disturbances by jerking violently (Johansen 1921; H. J. MacIsaac and T. C. Hutchinson, personal observations). Moreover, both fairy shrimp and copepods are unlikely to fall victim to *Mesostoma* mucous traps, while weaker swimmers, such as *Daphnia*, are susceptible. Indeed, a number of studies (Jennings 1957; Pickavance 1971; Adams 1980; Maly *et al.* 1980) have demonstrated that "mucus-trapping" is most effective against prey that either crawl (*Asellus*, *Gammarus*) or are poor swimmers (*Daphnia*). Differences in *Mesostoma* mucous production, which we observed across vegetation treatments, likely indicates different hunting strategies by the predator, although further work is necessary to substantiate this observation.

The high levels of predation on *C. riparius* that we observed in this study may not occur in open natural habitat because the larvae are often found in protective tubes, which may render them invulnerable to *Mesostoma* predation. However, chironomids in pond vegetation may be subject to high predation rates because they commonly occur without protective cases.

Refuges have generally been regarded as important factors permitting the long-term coexistence of voracious predators and their vulnerable prey (Murdoch and Oaten 1975; Woodin 1978, and references cited therein; Menge and Lubchenco 1981). In freshwater communities, rooted plants, benthic algae, stones, and sediments provide spatial refuge from piscine predators for small fish (Werner *et al.* 1983), insect larvae (Macan 1965), and amphipods (Pentland 1930). Our results with an invertebrate predator provide an interesting and contrasting variant on this theme. They demonstrate that the habitat complexity typical of vegetated littoral zones of arctic ponds may not necessarily promote prey survival. *Mesostoma* is an ambush predator, highly adapted to life along the bottom substrate of a pond and among submerged vegetation. It appears to be able to detect hydrodynamic turbulence generated by the movement of nearby prey. Once detected, the prey is quickly seized (Schwartz and Hebert 1982), immobilized, and the body contents are removed (Jennings 1957; Mead 1978). *Mesostoma* may encounter difficulty in capturing and immobilizing large-bodied prey (Pickavance 1971; Schwartz and Hebert 1982), such as *Branchinecta*. However, if prey were entangled in vegetation when encountered, *Mesostoma* could scavenge dead and dying organisms. Thus, although *Daphnia* are primarily planktonic, organisms venturing too close to macrophyte beds may become snared in the vegetation and possibly detected by nearby predators. Our results demonstrated that *Daphnia* were consistently captured and eaten at a higher rate when pond vegetation was present. Thus, the presence of *Mesostoma* in pond vegetation beds, both in the Canadian Arctic and in Africa (Mead 1978), is likely a behavioral consequence of increased predation success in this habitat. Similarly, the presence of many taxa of predatory invertebrates observed in lake macrophyte beds by Dvorak and Best (1982) may be attributable, in part, to high predation success.

It is not known whether *Mesostoma* mortality resulting from its attempts to capture *Branchinecta*, observed in our experiments, also occurs in nature. *Mesostoma* were frequently observed clinging to fairy shrimp, although predation success was negligible. If *Mesostoma* attack prey irrespective of species or size in nature, then frequent failed predation attempts on *Branchinecta* or any other invulnerable species could be of direct benefit to susceptible pond inhabitants, because the predator would be preoccupied and possibly wounded. Predation rates would then be lower than expected; hence, *Mesostoma* may not impact zooplankton dynamics to the extent previously believed (Maly *et al.* 1980; V. E. Dodson 1980, in Maly *et al.* 1980). It should be noted, however, that previous investigations of *Mesostoma* predation (Maly *et al.* 1980; Schwartz and Hebert 1982) did not attempt to assess vegetation effects, and hence may have underestimated predation potential.

We have demonstrated the importance of pond vegetation and prey behavior in affecting flatworm predation rates in laboratory experiments and speculated on its importance in natural systems. However, the exact extent of *Mesostoma* predation, and the impact of vegetation on it, have yet to be determined for arctic ponds *in situ*.

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