Abundance and Distribution of *Mysis relicta* in Moosehead Lake, Maine

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\textbf{Abstract}

\textit{Mysis relicta} is an exotic crustacean that was introduced into Moosehead Lake in 1975 to supplement the prey base for the resident lake trout (\textit{Salvelinus namaycush}). It was not until the 1984 that \textit{M. relicta} was first documented as being established in the lake. In 1995 public concern over poor landlocked salmon (\textit{Salmo salar}) growth due to low smelt (\textit{Osmerus mordax}) abundance initiated concern about the potential impacts of \textit{M. relicta} on zooplankton. During the summer of 1997, six deep water basins were sampled to determine the abundance and relative distribution of \textit{M. relicta}. Gillnetting was conducted in three basins to determine utilization of \textit{M. relicta} as a food source for lake trout and burbot (\textit{Lota lota}). Analysis of the 1997 data indicates a mean lakewide mysid density of approximately 0.93 mysids/m$^3$ with a standard error of 0.24. This density is relatively low when compared to other lakes that have had \textit{M. relicta} introduced, however, the species is present in low levels throughout the entire lake. Both burbot and lake trout were found to feed on \textit{M. relicta} throughout the water column, and may be exerting some control over the growth of the \textit{Mysis} population.

\textbf{Key Words:} burbot, exotic species, food habits, lake trout, \textit{Lota lota}, Moosehead Lake, \textit{Mysis relicta}, \textit{Osmerus mordax}, rainbow smelt, \textit{Salvelinus namaycush}, zooplankton
Adult Female *Mysis relict*ita
Introduction

Natural History

First described by Sven Loven in 1862, *Mysis relicta*, the opossum shrimp, is one of 20 freshwater shrimp species in the Crustacean order Mysidacea (Holmquist, 1963). Although *M. relicta* is generally considered to be an aquatic relict from the Pleistocene glaciation, derived from the marine species *Mysis oculata*, there have been alternative explanations of the origin of *M. relicta*. Holmquist (1963) stated that *M. relicta* is, in fact, quite distinct from *M. oculata*. She questioned whether *M. relicta* is actually a true relict species because it may have speciated well before glaciation. Furthermore, it may have even been distributed in North American freshwaters before glaciation (Holmquist, 1959). Ricker (1959) proposed two main hypotheses regarding the natural distribution of aquatic glacial relicts: (1) *M. relicta* was found in ocean basins until continental uplifting created basins which gradually filled with freshwater, changing them to lakes; (2) glaciers pushed the species from salt water into lakes along the margin of the last glaciation. More recently, Vainola (1986) examined the phylogenetic relationships of *M. relicta* and other related species, finding three sibling species of *M. relicta*, all three of which were genetically most closely related to the marine species *Mysis litoralis* rather than *M. oculata*. The investigation also indicated the divergence of the three *M. relicta* sibling species well before the Pleistocene glaciation. Despite *M. relicta*’s somewhat unclear history, its importance of in aquatic food webs is well documented and has become of particular interest to many fisheries managers.

With a circumpolar distribution, *M. relicta* is found throughout the northern latitudes (above the 42° N parallel) of North America, Scandinavia, and Russia (Holmquist, 1959). Some of the lakes to which they are native in North America include the Great Lakes, Green Lake, Trout Lake, and Lake Geneva in Wisconsin, the Finger Lakes in New York, and some Canadian shield lakes. In the past 70 years the natural distribution of *M. relicta* has been increased by its introduction into freshwater lakes for the purpose of increasing the forage base of sport fisheries. The species’ distribution is limited by its habitat requirements which include cold, deep, oligotrophic, and well-oxygenated waters.
Basic Biology

Anatomy and Physiology

*M. relicta* somewhat resembles a miniature crayfish, although there are many differences in structure. Mysids have a thinner carapace that does not completely cover the thorax, and walking legs are replaced with long, thin, setose appendages used for swimming, feeding, and respiration. The first two pairs of appendages are used for raptorial zooplankton feeding or straining phytoplankton and particulate debris. Respiration, which is most efficient during swimming and feeding, occurs through the thin carapace. One particularly interesting feature is the presence of a statocyst in each of the uropods. The stalked eyes are large, compound, and well developed for precise photoreception. Mature males can be distinguished by their abnormally long and specialized fourth pleopod which is the gonopod. Mature females develop a brood pouch at the base of the last pair of legs, generally reach larger sizes, and are more abundant. They reach a maximum size of about 30 mm, although sexually mature individuals are generally about 15-18 mm (Pennak, 1989).

Vertical Migration

One of the more salient features of *M. relicta*’s life history is its vertical migration. Primarily benthic and planktonic, *M. relicta* exhibit some of the most extensive and rapid diel vertical migrations of all freshwater crustaceans (Pennak, 1989). Generally, they migrate to the metalimnion when light levels decrease at dusk and then return to deeper waters with the increasing light levels at dawn. Light is the primary factor influencing vertical migrations of *Mysis*, however, it is still unclear whether they migrate along with an optimal light intensity or if they cue off a certain change in light intensity (Beeton, 1960). Temperature also effects migration as *M. relicta* will migrate up to the surface waters unless they encounter an established thermocline which they will stay below (Beeton, 1960; Beeton & Bowers, 1982). It has also been demonstrated that smaller juvenile mysids often lead the upward migration, rise highest, and are among the last to descend (Morgan, 1980; Beeton & Bowers, 1982). The rate of ascent (0.8m/min) and descent (0.4m/min) makes it possible for *M. relicta* to reach metalimnetic feeding grounds quite quickly.
even in the deepest portions of the Great Lakes (Beeton, 1960). The factors that determine the extent of the upward migration include; prevailing light conditions (e.g. moonlight), temperature, lake morphometry, stage of maturity, and lake trophic status (Beeton, 1960; Lasenby, 1991). It is generally believed that the evolutionary significance of the vertical migration in *Mysis* is similar to many zooplankton, where natural selection has tended toward a balance of metabolic rate related to temperature, feeding opportunities, and predation pressure in high light conditions on the migrating species (Beeton & Bowers, 1982).

Morgan and Threlked (1982) found evidence of size-dependent horizontal migration in *M. relicta*. In Lake Tahoe, adults stayed in deep basins year round while many newly hatched juveniles migrated into shallower waters for a few months and then returned to deep water. It is possible that because of smaller size, the juveniles are harder to see and can occupy a separate habitat without increased predation by fish. The extensive horizontal and vertical migrations by *M. relicta* even in large lakes (i.e. Tahoe, and the Great Lakes) suggests that most populations may not exist as sub-populations, but rather as a unit (Morgan, 1985).

**Feeding**

*Mysis relicta* is an opportunistic feeder with both predatory and filter-feeding habits (Lasenby and Langford, 1973). At night, when *M. relicta* is found throughout the water column they often feed heavily on zooplankton. Zooplankton densities and community composition may significantly shift due to selective predation by *M. relicta* (Zyblut, 1970; Richards et al., 1975; Goldman et al., 1979; Kinsten & Olsen, 1981; Langeland, 1981; Morgan et al., 1981; Reiman & Falter, 1981; Threlked, 1981; Murtaugh, 1983; Nero & Sprules, 1986). There is a strong relationship between *M. relicta's* ability to capture certain prey and the feeding rates on those prey, suggesting that ease of capture largely determines prey preference (Cooper & Goldman, 1980; Ramcharan et al., 1985). Studies indicate a prey preference of large cladocerans > small cladocerans > copepods > and cyclopoids; however, mysids have been shown to feed on just about anything they can handle, including smaller mysids (DeGraeve & Reynolds, 1975; Lasenby & Furst, 1981; Bowers & Vanderploeg, 1982; Grossnickle, 1982).
Laboratory experiments by Cooper and Goldman (1982) indicate little effect of environmental conditions on *M. relicta* predation. Predation rates were similar during dark and light conditions, and also for different temperatures. In contrast, Ramcharan and Sprules (1986) detected higher feeding rates by *M. relicta* on *Daphnia* and *Diacyclops* during higher light conditions. Zooplankton abundance and composition has been shown to be inversely related to *M. relicta* selectivity and clearance rates (Cooper & Goldman, 1982; Folt et al., 1982). Overall, it appears the impact *M. relicta* may have on zooplankton communities is inversely related to the number of fish species feeding on the *Mysis* as well as the level of predation on them (Furst, 1981).

During the day when *M. relicta* are found within 1 or 2 m of the bottom or if zooplankton are scarce or absent, mysids will feed on descending particles (i.e. feces and phytoplankton), detritus, and benthic organic matter (Bowers and Grossnickle, 1978). One of the reasons why *Mysis* was chosen for introduction to improve fisheries was the idea that the benthic feeding of *M. relicta* would utilize benthic nutrients that would otherwise be lost (Morgan, 1985). In this capacity *M. relicta* was seen as an “energy elevator” because it could transport dormant energy back to pelagic fish who feed upon *Mysis* (Lasenby, 1991). While this may be true if benthic feeding by *Mysis* is high enough, there are other mechanisms by which benthic feeding may increase lake productivity. Their activity on the lake bottom may stir up sediments, releasing phosphorus back into the water (Kasuga and Otsuki, 1984). Furthermore, when mysids migrate nightly to shallower waters, their fecal and metabolic excretions can directly increase phytoplankton productivity (Maderia et al., 1982).

Due to their diel vertical migrations, the impacts of mysid grazing is often felt throughout the lake and can play an important role in structuring the limnetic food web (Grossnickle, 1982). Their ability to adapt to locally available food suggests that they often maintain an optimal growth rate (Morgan, 1985). The mobility of mysids and their high growth rates, coupled with the ability to switch food sources when zooplankton are depleted, may be why *M. relicta* has enjoyed such success in many of the lakes to which it has been introduced.
Predators

*M. relicta* is prey for a large number of fish species which is the primary impetus for its introduction in freshwater lakes. Depending on the fish composition of a particular lake, *Mysis* predators include: lake trout (*Salvelinus namaycush*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), kokanee salmon (*Oncorhynchus nerka*), burbot (*Lota lota*), rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and various coregonids (*Coregonus* sp.) (Gosho, 1975). Most frequently, juvenile stages of coregonids and salmonids extensively utilize *M. relicta* during their transition from planktivory to piscivory (Morgan, 1980). Some fish populations (i.e. lake trout in some smaller Canadian lakes) subsist almost entirely on *Mysis* (Pennak, 1989); however, the same fish species may not necessarily switch to and utilize introduced populations in another lake. Although *Mysis* are a high energy food item (20mm adult = 20 calories (Lasenby & Langford, 1972)) and should theoretically be an important food item, their vertical migrations often preclude extensive habitat overlap for certain fish species. In a study of *Mysis* introductions in 50 Swedish lakes, *M. relicta* had positive effects on growth or condition of primarily benthic feeding fish while pelagic fish were negatively affected (Furst et al., 1985). Furthermore, *Mysis* may out-compete potential predators (i.e. kokanee salmon and smelts) for their primary prey of zooplankton (Johannsson et al., 1994; Lasenby et al. 1986).

Reproduction

Mysids reach maturity after 1 to 4 years and reproduction can occur once or multiple times a year, depending on the temperature and productivity of the lake (Morgan, 1985). In extremely cold and unproductive lakes, the lifespan is longer than in more productive or warmer lakes, reaching a maximum of four years (Beeton and Gannon, 1991). Sexes can first be distinguished at 7-8mm but sexual maturity does not occur until 12-15mm. Mating generally occurs in the late fall, although some populations have exhibited continuous reproductive behavior. Once mature males locate females in the proper condition they either grasp them by the tail end and either insert the penes into the marsupium and release sperm, or they release sperm in adjacent water where the females use their appendages to sweep the sperm into the marsupium (Mauchline, 1980).
Immediately following sperm release, the female extrudes her eggs into the marsupium for direct fertilization. Males appear to mate once and die, while females have been shown to mate more than once. Embryos develop in the female’s marsupium (hence the name opossum) for a duration of up to 4 months. Brood size is shown to be positively related to female size (Johannsson, 1995), averages around 20 with a maximum size of about 40 embryos; however, the number often decreases because not all of the embryos survive the brooding (Morgan, 1985). Embryo development is highly variable, ranging from 4 months to over 9 months depending on the water temperature during development (Berrill, 1969; Lasenby & Langford, 1972). Young are released in early spring at a size of 3-4 mm, where they undergo direct development to the adult form (Lasenby & Langford, 1972). Before reaching sexual maturity, they undergo up to 12 molts, including one that takes place immediately preceding mating (Morgan & Beeton, 1978). Growth varies between lakes depending on environmental and biological conditions but averages about 1 mm per year with somewhat faster growth in the summer (Gosho, 1975). Morgan (1985) examined several length-weight data sets and found that dry weight increased with the cube of total length.

**Cause for Concern - Salient Introductions**

The importance of mysids to fisheries has become an issue of considerable concern during the last 30 years as numerous studies of introduced *M. relicta* populations have documented significant and often detrimental impacts on lake ecosystems (Nesler and Bergersen, 1991). The introduction of exotic *M. relicta* is similar to other unsuccessful efforts to manage freshwater systems with introduced exotic species. In most of these cases, a sound theory for introducing an exotic species for some beneficial results (i.e. increased forage base) coupled with initially successful results triggered widespread adoption of these practices. Unfortunately, many of these early success stories eventually became failures which actually adversely affected those species that were supposed to benefit.

Knut Dahl first proposed the introduction of *Mysis* into unproductive Norwegian lakes in 1910 (Northcote, 1991). The idea that *M. relicta* could be introduced to enhance food resources
for lake whitefish (*Coregonus clupeaformis*) was proposed in North America by Clemens et al. (1939) when they recommended that both *Mysis* and *Pontoporeia* be added to the lakes in the Okanagan region of British Columbia. The case for introducing *Mysis* was furthered by Larkin (1948) who suggested they might augment sparse bottom fauna in some alpine lakes, considering the importance of mysids as forage for fish in lakes in which they are naturally found.

The first introduction of *M. relicta* into a lake took place at Kootenay Lake in 1949, where *Mysis* were added as additional forage for resident salmonids (Sparrow et al., 1964). It was hoped that *Mysis* would fill an apparent forage gap between zooplanktivory and piscivory (later named the ‘*Mysis* niche’) for intermediate sized rainbow trout. Although the growth of the targeted species, rainbow trout, did not change, growth rates and size of large kokanee significantly increased. This successful introduction became the rationale for numerous introductions throughout North America and Scandinavia. The success, however, was temporary. Nearly two decades later the abundance of *Daphnia* started to decrease, negatively impacting both young rainbow trout and kokanee in Kootenay Lake (Northcote, 1972).

Lake Tahoe was one of the unfortunate lakes stocked with *M. relicta*, soon after the apparent success in Kootenay Lake. During 1963-1965 over 330,000 mysids were stocked from Waterton Lake to increase the available forage for another non-native species, kokanee salmon. As soon as 3 - 4 years later, there were marked declines in the abundance of two cladocerans, *Daphnia rosea* and *Daphnia pulicaria*, with a third, *Bosmina longirostris*, declining 2 years later (Richards et al., 1975). While both *Mysis* and kokanee predation were responsible for the initial decline of these cladoceran species, cultural eutrophication was held responsible for not allowing these zooplankton communities to recover (Goldman et al., 1979). Although kokanee did exhibit increased growth rates initially, both the mean weight and number of spawners began to decline. Lake trout, also present in the lake, switched their food habits to include large amounts of *M. relicta* when they were abundant, although when *Mysis* were sparse lake trout condition deteriorated (Morgan et al., 1978). Admittedly other factors such as cultural eutrophication and
increased fishing pressure have had their effects on Lake Tahoe, but the loss of the three cladocerans ultimately impacted the fishery for the worse.

One of the better known introductions of *M. relicta* was in Flathead Lake. *Mysis* were not directly stocked into the lake but rather were stocked in Ashley, Swan, and Whitefish lakes which are found upriver of Flathead. *Mysis* then drifted downriver from these lakes. Soon after they were first found in 1981, the annual abundance of cladocerans and some copepods began to decline while *Mysis* levels increased (Spencer et al., 1991). As the zooplankton levels decreased, the number non-native kokanee spawners also began to decrease dramatically. Even more visible was the link further up the food chain whereby the large numbers of bald eagles and grizzly bears that once had gorged on the spawning kokanee were forced to shift to other foods in the autumn. Furthermore, other feeding locations along the autumn migration route of the bald eagle may not be adequate and increased mortality may result in this highly visible bird population (Spencer et al., 1991). These interactions in the Flathead Lake ecosystem comprise one of the most apparent examples of the trophic cascade idea. The story is not totally negative because lake whitefish and small lake trout have become more abundant. These fish are both benthic feeders and are known to feed heavily on *Mysis*. Despite this, the Flathead Lake ecosystem has been dramatically altered by an indirect *M. relicta* introduction.

Unfortunately, a large majority of these attempts to increase the available forage base failed. *M. relicta* altered the trophic structure in many of these lakes by modifying benthic, phytoplanktonic, zooplanktonic, and fish communities (Lasenby et al., 1986). Although *M. relicta* introductions have ceased, there is no current method for removing this species from the many lakes in which it is now found. Northcote (1991) suggested four possible control methods for introduced *Mysis* populations: 1) manipulation of thermal stratification, 2) manipulation of turbulence and upwelling, 3) increased lake productivity, and 4) biological controls. Of these, biological controls have received the most attention, focusing on predatory fish species that have significant habitat overlap with *M. relicta* or those that exhibit diel vertical migrations (Martinez and Bergersen, 1989). The irony of this proposition lies in the introduction of another exotic, such as
a benthic fish predator, to attempt to control *Mysis*. Experience has shown that great caution should be exercised with exotic introductions (Li and Moyle, 1981) and therefore, it is likely that these exotic *Mysis* populations will remain.

**Impetus for Study**

During the last 100 years, the fishery in Moosehead Lake located in north-central Maine, around which much of the local economy is centered, has been one of the premier coldwater game fisheries in the northeast United States. Recently, the average size of the three primary game fish (brook trout *Salvelinus fontinalis*, landlocked Atlantic salmon *Salmo salar*, and lake trout) and the abundance of brook trout and salmon has declined below historical levels. This change in the fishery resulted in a decline in recreational use (Paul Johnson, personal communication). As a result, much of the economy of the two local towns, Greenville and Rockwood, ME, which rely heavily on fishing-based tourism, has been adversely impacted. In 1995 many local business and personal interests formed the Moosehead Lake Fishery Coalition (MLFC) to identify problems and develop management strategies in hopes of improving the fishery.

One publicly cited possibility for the decline in the fishery was a decrease in the zooplankton levels found in Moosehead Lake. As one of the key components of the food web in any lake, it is important to know the status (including abundance and diversity) of this food source for many of Moosehead’s fish and other aquatic organisms. In particular, there was concern that *M. relicta*, introduced in 1975, may be related to changes or reductions in zooplankton levels (Anonymous, 1995). As with *Mysis* introductions in many other lakes, this introduction was an attempt to increase the available forage for the native lake trout.

Evidence that *M. relicta* had become established in Moosehead Lake was collected in 1984, when the biologists from the Maine Department of Inland Fisheries and Wildlife (IF&W) found *Mysis* remains in deep water trawls (Anonymous, 1995). Concern about *M. relicta* stems from some of the negative incidents mentioned earlier in this document. However, at present there is no link between the fishery decline and the *M. relicta* introduction in Moosehead. Currently, there is no information about the abundance or distribution of *M. relicta* in Moosehead Lake. Therefore, as
part of a thorough investigation of the current fishery, establishing information about \textit{M. relicta} is essential.

Specifically, the objectives of study were to determine estimates of the abundance as well the distribution of \textit{Mysis} throughout Moosehead Lake. Also of interest was determining the utilization of \textit{M. relicta} by the two primary benthic fish predators, lake trout and burbot.

\section*{Study Site}

\subsection*{Lake Characteristics}

Moosehead Lake in central Maine, is one of the largest lakes east of the Mississippi River and is one of the few large lakes whose game fish consist solely of lake trout, landlocked Atlantic salmon, and brook trout. It is a large (30,500 hectares), oligotrophic lake with a maximum depth of 74.2m and a mean depth of 16.6m (AuClair, 1982). It is of glacial origin and is relatively unbuffered. The shoreline development index value of 4.96 reflects its highly convoluted shoreline, which includes many well-defined coves and bays. The lake water has low nutrient concentrations, scarce aquatic vegetation and algae, and the bottom sediments are primarily inorganic. Stratification occurs generally from June through September, with frequent mixing within the epilimnion due to the prevailing northwest winds. Maximum temperatures reach $21^\circ \text{C}$ in the epilimnion, while the hypolimnion maximum temperature rarely exceeds $10^\circ \text{C}$, and summer hypolimnetic oxygen levels are constant throughout the lake with values averaging about 9.0 mg/l. Two dams at the major outlets regulate the lake level throughout the ice-free period (AuClair, 1982).

\subsection*{Biological Communities}

The fishery in Moosehead Lake consists primarily of lake trout, landlocked Atlantic salmon, brook trout, and burbot, although there are isolated populations of recently illegally introduced yellow perch (\textit{Perca flavescens}), white perch (\textit{Morone americana}), and smallmouth bass (\textit{Micropterus dolomieu}) (AuClair, 1982). Lake trout, brook trout, and lake whitefish are the
only native sportfish. In 1879, landlocked salmon were introduced and have since established naturally reproducing stocks although supplemental stocking still takes place. Rainbow smelt were introduced in 1892 to provide an additional forage base for all of the salmonids. Since their introduction, rainbow smelt have become the primary forage for all three salmonids. Introduced yellow perch (late 1950’s), smallmouth bass (1975) (AuClair, 1982), and white perch (Paul Johnson, personal communication) may compete with smelt and brook trout, although no direct evidence of this exists.

Although the introduction of landlocked Atlantic salmon may have reduced slightly the historical brook trout population via competition, all three salmonids have enjoyed relatively successful coexistence over the last century. A survey in 1944 (Cooper and Fuller, 1945) found that all three salmonids preyed almost exclusively on rainbow smelt. Although there are differences in the preferred habitat of lake trout, salmon, and brook trout, there is a significant overlap in feeding ranges, especially between depths of 9 and 18 meters (Harvey & Warner, 1970). Because rainbow smelt are also found in this area, interspecific competition for both smelt and space is likely. However, it is apparent that the smelt population has been abundant enough for all three game fish to coexist. This is supported by the fact that 33 of 50 of the lakes considered to be the best fishing lakes in Maine had three or more smelt-eating species in coexistence with a steady smelt population (Havey & Warner, 1970).

Recently, there is evidence of a declining smelt population (Anonymous, 1995). This is of substantial concern, considering Moosehead Lake salmon growth rates and abundance are directly related to smelt abundance (Sayers et al., 1989). Sayers et al. (1989) also speculate that an increase in lake trout abundance at the same time may be reducing the smelt population. It is also possible that the smelt population has had some extremely small year classes, resulting in the apparently wide fluctuations in abundance. The species has been shown to exhibit population swings of up to an order of magnitude from year to year without any apparent relation between stock size and recruitment (Kircheis & Stanley, 1981) or other causes such as predation, competition, fishing pressure, or disease (Smith, 1972; Havey, 1973). Therefore, although they
are the primary forage for game fish in many lake systems, these population swings often limit the reliability of rainbow smelt as a primary prey (Kircheis & Stanley, 1981; Kirn & LaBar, 1996).

The zooplankton community in Moosehead Lake is typical of many similar deep, oligotrophic lakes in Maine and consists of cladocerans (primarily *Daphnia* but also *Bosmina, Ceriodaphnia, Leptodora, Polyphemus*, and *Sida*), copepods, and rotifers (Cooper & Fuller, 1945; Anonymous, 1995). Zooplankton sampling was conducted in 1995 by the Maine IF&W and analyzed by Dr. David Courtemanch of the Maine Department of Environmental Protection. The results showed a wide range of size classes of many of the zooplankters found in comparable coldwater lakes in the region (Anonymous, 1995). When these results were compared to the only other plankton sampling done on Moosehead (Cooper and Fuller, 1944) no statistical differences were found. The presence of several large cladoceran species indicates there are zooplankton available for consumption by smelt and juvenile salmonids alike.

**Methods**

*Mysis* Sampling

*Mysis* samples were collected between June 12 and September 5, 1997 from six primary and two additional sites in Moosehead Lake. Thirty-one sampling events were conducted, with each of the six primary sites sampled twice monthly. The six sites were located in the deepest water of the six major deep-water basins in the lake (Figure 1). All sampling events took place at least 1 hour after dusk during the 2 weeks between the last quarter and first quarter moon phases when there was no moon present. At each site sampled, cloud coverage, wind speed, and wind direction were recorded after the anchor was set. Four vertical hauls were taken from within 1m of the bottom with a *Mysis*-style vertical haul net (Nero & Davies, 1982; Lawrence Enterprises, Seal Harbor, ME). Each haul was rinsed into a separate collection jar and preserved with 95% ethanol. All individuals in each sample were counted, grouped into 5mm classes, and sex was determined for individuals over 15mm. Juvenile smelt and *Leptodora* were also counted.
Fish Stomach Analysis

During summer, the IF&W annually conducts deep water gillnetting in two basins at the southern end of the lake (Figure 1). Both of these sites were primary Mysis sampling sites (Birch Island and Sugar Island). An additional site (Farm Island) was added to the 1997 netting regime and this was also located in a basin where Mysis sampling occurred. Six experimental nylon gill nets of common stretch mesh sizes from 25.4 to 63.5 mm (1 to 2.5 in.) were used. Each net consisted of four 15.24 m (50 ft.) panels and was 1.8 m (6 ft.) deep. Thirty total bottom gillnet sets were fished overnight during August and September, in depths of 15.24-30.48 m, 30.48-45.72 m, and 45.72-60.96 m (50-100 ft., 100-150 ft., and 150-200 ft.). For each fish captured, length and weight were measured, otoliths were collected for aging, sex and maturity was determined, and stomachs were immediately dissected and contents were quantified using occurrence methods.

Results

Mysis

Mean densities of *M. relicta* at each of the six primary sites was determined by averaging values from each of the sampling events. Minimum and maximum mean densities for all sampling events in 1997 ranged from 0.0507 mysids/m³ to 7.3639 mysids/m³, while the lake-wide average of all samples was 0.93 mysids/m³ with a standard error of 0.24. Captured Mysis sizes ranged from newly hatched (3-4mm) up to 31mm which is near the maximum length documented for the species. In general, mature females were more numerous and larger than mature males.

*Mysis* densities varied considerably among the six sites (Figure 2). The Moose Island site had an extremely large standard error due to one of the sampling events where *Mysis* were four times more numerous than for any other sampling event. There were no significant trends although there appears to be some increase from the northern to southern sites (Figure 3). There were significant differences between the densities at the sites but no differences between sampling time intervals (Friedman nonparametric two-way anova, P>0.005). The mean summer Birch Island (and Moose Island without 7/27) density was significantly higher than the North Bay, Farm
Island, and Sugar Island sites (paired t-tests; N=20, P<0.05). *Mysis* of all size classes (<5mm, 5-10mm, 10-15mm, and >15mm) were found at all sites (Figure 4). It is possible to see the decrease in juveniles (5-10mm) and the related increase in the early adults (10-15mm) and the adults (>15mm) through the summer. Mean densities of the smallest group (<5mm) increased to a maximum in August, indicating peak hatching during early August.

Other enumerated organisms collected in the vertical hauls included juvenile smelt and the cladoceran *Leptodora*. Juvenile smelt were present in the first and second sampling events at all six sites in low but relatively similar densities of 0.015 - 0.04 smelt/m³. Over the approximately 1.5 months that they were captured, the smelt grew to the point where they could presumably avoid the vertical haul net. The large cladoceran *Leptodora* was also found at all sites and throughout the summer. However, there was considerable variation both within and among sites (Figure 5).

A total of 65 lake trout and 46 burbot were captured in the summer deep water gillnetting. Also caught were round whitefish (*Prosopium cylindraceum*), longnose suckers (*Catostomus catostomus*), white suckers (*Catostomus commersoni*), and two smelt. Analysis of the food habits of lake trout and burbot were compared with results from 1990-1992 and 1995-1996. In 15 - 30 m of water, *Mysis* occur in 5% to 18% of lake trout stomachs (Figure 6). However, in the deeper waters (30 - 45 m) percentage occurrence was higher, particularly during the past 3 years (58% - 85%). It also appears that the smelt population was absent or very weak during 1995-1996 as smelt remains were only found in 10% of all lake trout stomachs examined. Most of the *Mysis* eaten by lake trout in 1997 were found in fish smaller than 360 mm, although only a quarter of the fish caught were larger than 360 mm (Figure 7).

*Mysis* utilization by burbot was quite high and consistent over the past 7 years, especially in the deeper water (Figure 8). The absence of smelt in burbot stomachs during 1995-1996 was similar to lake trout. In 1997, over 60% percent of all burbot less than 380mm were found with *Mysis*, compared to only 17% of lake trout less in the same size range. The narrow length-frequency graph of the gillnetted burbot indicate either some well-defined gear selectivity, a narrow size structure of burbot, or both.
Discussion

It is evident that the *M. relicta* population introduced into Moosehead Lake has become established throughout the lake and is now a part of the aquatic community. The observed mean densities at the six sites show some spatial variation which is to be expected in such a large lake; however, *Mysis* levels are well below densities in lakes where *M. relicta* has caused significant changes in zooplankton and fish communities (Table 1). The densities in these lakes, where significant changes in community structure have taken place, are at least 30 times higher than those found in Moosehead Lake. Swan and Ashley Lakes in northwestern Montana have densities very similar to Moosehead (Leathe, 1984). In these two lakes and possibly Moosehead, *M. relicta* has become an important part of the food web by providing supplemental forage for the resident lake trout and burbot, yet it has little impact on the zooplankton levels.

The mean *Mysis* densities at the Birch Island (and Moose Island without 7/27) are significantly higher than those at the North Bay, Farm Island, and Sugar Island sites. Because Moosehead Lake is made up of six separate basins of deep water rather than one continuous basin, the *Mysis* population may not be as uniform as in single basin lakes such as Flathead Lake. The three sites with the highest densities are: Rockwood, the site of introduction and also the largest inlet into the lake (Moose River), and Birch and Moose Island sites, located in the more highly developed Southern quarter of the lake. Higher nutrient inputs in these three basins from the Moose River and developments along the Southern shoreline may be related to the higher *Mysis* densities. Higher primary productivity due to the high nutrient input may lead to higher secondary productivity, thus providing a larger zooplankton forage base for the *Mysis*.

Life history of *Mysis* populations is important because it is often linked to aspects of their feeding and distribution in a lake (Lasenby, 1991). *Mysis* populations have been shown to have life cycles of 1 to 4 years, depending on environmental conditions (Gosho, 1975). Moosehead is a relatively cold and unproductive lake, similar to those with longer mysid life cycles. All life stages of *M. relicta*, from egg to freshly hatched to unusually large adults over 30mm, were observed during the summer sampling. One particularly interesting sampling event captured significantly
higher juvenile mysids than all other dates and sites. Sampling technique was standard this night so it is speculated that a cohort may have just hatched and was unusually congregated. There appeared to be three major cohorts of *M. relicta* sampled throughout the summer with members of both sexes present. Also noted was the presence of unusually large female mysids (> 25mm) which may represent a small fourth cohort of 3-year old shrimp. Because males die after mating, the presence of cohorts of mature males in ratios similar to mature females throughout the summer may indicate a 2-year life cycle, although some females may survive a third year. The 2-year life cycle of this population indicates a slower growth rate than in most other lakes containing *Mysis* with shorter time to maturity.

Plankton densities for 1997 were not analyzed; however, abundance of the large cladoceran, *Leptodora*, was documented. Although *Leptodora* densities were spatially and temporally variable (Figure 5), *M. relicta* have not eliminated them from Moosehead Lake as in Flathead Lake (Spencer et al., 1991). The cladoceran *Polyphemus* was also relatively abundant. Both of these cladocerans are relatively large zooplankters which are commonly eaten by smelt and *Mysis*. Zooplankton data sets exist from 1944, 1995, and soon 1997. Although abundance of the three most abundant zooplankton groups (cladocerans, copepods, and rotifers) varied between the studies in 1944 and 1995, there were no statistical differences. The abundance and diversity of the zooplankters found in Moosehead Lake in 1995 indicates that this food source is sufficient to support the smelt and *Mysis* populations (Anonymous, 1995). Changes in plankton levels and community composition is one of the more important measures of the impact of *Mysis*; therefore, zooplankton monitoring should be continued.

The fish community in the lake could have been affected by a high density *Mysis* population if it were to significantly alter the zooplankton community. Since the smelt population has been experiencing cycles of high and low abundance, it is possible that *M. relicta* could have been out-competing smelt for the available zooplankton. However, smelt populations have also been known to crash periodically without relation to typical causes (Smith, 1972; Havey, 1973). Because of the heavy dependence of landlocked salmon and lake trout on smelt, any *Mysis* induced
zooplankton change could quickly send the forage base to dangerously lower levels. Alternatively, if the *Mysis* population is stable, they could provide additional forage to both the lake trout and the smelt populations. Brownell (1970a) reported utilization of *Mysis* by smelt in Cayuga Lake, and Youngs and Oglesby (1972) also found that smelt and young lake trout fed heavily on *M. relicta*. Similarly, Gosho (1975) noted that in Grindstone Lake, Minnesota, predation by smelt was believed to suppress the growth of the *Mysis* population. It may be possible that together, the smelt, lake trout, and burbot populations may be controlling the *Mysis* levels. While there are relatively high levels of utilization of *Mysis* by lake trout and especially burbot, there are no food habit data of smelt to support this idea.

The stomach analysis of both lake trout and burbot support ideas generally held about utilization of *M. relicta*. For both species there is higher consumption of *Mysis* by fish in water over 30 m, where *Mysis* abundance is highest. Although few lake trout caught in water shallower than 30 m had eaten *Mysis*, between 55% and 84% of the gillnetted lake trout in deeper water contained *Mysis*. It is interesting to note that in the deep water in 1995-1996 there were no smelt in 27 lake trout; however, almost 85% of these same fish stomachs contained *Mysis* (Paul Johnson, unpublished data). This could indicate that when smelt are not present, lake trout will feed more heavily on *M. relicta*. In this case, the *Mysis* population could provide an alternative food source for lake trout, which may reduce the impact of a weak smelt year class. Burbot, on the other hand, have been consuming *Mysis* consistently for at least the last 7 years. The lower percentage occurrence in the burbot caught from 15 - 30 m can be attributed to the likely lower abundance of *Mysis* in those water depths. It is apparent that *Mysis* is one of, if not the most important food item for burbot.

This *Mysis* population survey fills an important void in the data of the Moosehead Lake fishery. Although this study was conducted primarily to determine the abundance and distribution of *M. relicta* in Moosehead Lake, it has led to possible insights about the Moosehead Lake food web and has also begun to answer questions regarding the role of *M. relicta* in this lake’s ecosystem. At this point in time, it appears that the *Mysis* population growth may be restricted by
predation of the abundant populations of lake trout and burbot. Other factors such as basin morphology, lake productivity, and smelt population dynamics may also contribute some control. One question, in particular, that remains is the variability of the smelt population. Future research efforts should focus on smelt population attributes such as recruitment, survival, growth, and food habits, as well as the availability of adequate spawning sites.

This initial *Mysis* data set can serve as a start for a long-term monitoring program of the mysid population, its effect on zooplankton and consequently the rest of the Moosehead Lake food web. While most studies of *Mysis* have dealt with lakes where major trophic changes have already occurred, there are few studies of introduced mysid populations that did not result in adverse impacts. The *Mysis* population in Moosehead Lake has been established for nearly 20 years and may have stabilized. Conversely, the lake’s salmon, brook trout, lake trout, and smelt populations have recently been changing; circumstances often linked to unbalanced predator-prey relationships. Furthermore, minor changes in a lake’s biotic community provide opportunities for an exotic species such as *M. relicta* to exploit its new environment years or even decades after its introduction. Therefore, continued monitoring of *Mysis* is important, if for nothing more than documenting a relatively benign *Mysis relicta* introduction.

**Recommendations**

**Sampling Interval**

Ideally, *Mysis relicta* sampling should occur yearly for the next 3 - 5 years, at which time the required sampling interval should be reevaluated. The importance of frequent sampling is necessitated as mysid populations have been shown to increase dramatically in only a year. After a series of annual data are collected it should be easier to detect trends and the sampling interval can be reevaluated on this basis.

Due to potentially limiting resources (i.e. funds, time constraints, available help) sampling may only be possible every 2 - 3 years. If monitoring of this *Mysis* population is to be of any predictive use, sampling intervals should not be longer than 3 years (especially because only one data set currently exists).
Sampling Sites

Of the six major sites sampled regularly during the summer of 1997, at least two (preferably three) should be sampled during future monitoring efforts. The two sites that should be monitored are the Moose Island and Rockwood Narrows sites. Although any of the six (seven including the Kineo deep hole) sites are suitable for sampling, the Moose Island and Rockwood sites are probably the easiest to access and sample at night. It is also important to sample at these sites because they represent areas that have the best *Mysis* habitat.

Sampling Frequency

The frequency of sampling for any monitoring year need not be extreme. It should be adequate to sample each site three or four times during the summer months. An ideal schedule would be to sample two or three sites every month (near the new moon for best moonless nights) for 3 or 4 months. This should give a good representation of temporal changes over the summer while also eliminating potential over- or underestimates resulting from cluster sampling at unusual high or low densities. Although the 1997 study indicates significant differences in *Mysis* densities between sites, so two or three sites should be adequate because the density levels are so low.

General Recommendations

1). Winter creel census stomach analyses should consider *Mysis* a potential prey item and should pay close attention for remains (as winter utilization of *Mysis* is currently unknown).

2). All fish collected for research purposes should be examined carefully for *Mysis* remains.

3). The Moosehead Lake management plan should include monitoring programs for *Mysis* and zooplankton.

4). Determine the utilization of *Mysis* by smelt and juvenile lake trout. The relationship between these two fish species and *Mysis* may be important to the abundance and growth rate of lake trout as well as landlocked salmon in the fishery.

Acknowledgments

This study is the primary research project of my Master of Science degree program at the University of Minnesota. The study was conducted in cooperation with the Moosehead Region, Maine Department of Inland Fisheries and Wildlife. Regional biologist, Paul Johnson was involved in the formation of the project and assisted throughout the study. Funding was generously provided by the Moosehead Lake Fishery Coalition. I want to thank my advisor Dr. Ira Adelman for his assistance, guidance, and patience. I would also like to thank everyone involved in the project including all those who volunteered to help with the night sampling and those to which I spoke at great length to about *Mysis*: Paul Johnson, Dr. Bud Fackelman, Shandor Szalay, and the members of the MLFC.
Table 1: Reported maximum densities for natural and introduced populations of *Mysis relicta*, (modified from Lasenby 1991).

<table>
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<tr>
<th>Lake</th>
<th>Location</th>
<th>Density (#/m^3)</th>
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<tr>
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<td>Maine</td>
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Figure 1: Location of sites for *Mysis relicta* sampling and summer deep water gill netting.
Figure 2: Mean mysid densities (#Mysis/cubic meter) + 1 standard error at each sampling event grouped by site. Sites are listed from North to South (left to right).
Figure 3: Mean summer densities ± 1 standard error of *M. relicta* at the primary sampling sites. The far right column was calculated without the July 27 sample.
Figure 4: Length frequencies of *M. relicta* normalized on y-axis to 100% and grouped by time interval.
Figure 5: Density of *Leptodora* at each sampling event grouped by site. Sites are listed from North to South (left to right).
Figure 6: Percentage occurrence of smelt and *Mysis* in gillnetted lake trout (of those with food in the stomachs) in 15-30 m and 30-45 m of water.

Data from 1990-1992 and 1995-1996 are from previous investigations.
Figure 7: Length-frequency chart of gill netted lake trout with the frequency of occurrence of *M. relicta* found in stomachs of lake trout within each size class.
Figure 8: Percentage occurrence of smelt and *Mysis* in gillnetted burbot (of those with food in stomachs) in 15-30 m and 30-45 m of water.

Data from 1990-1992 and 1995-1996 are from previous investigations.
Figure 9: Length-frequency chart of gill netted burbot with the frequency of occurrence of *M. relictia* found in stomachs of burbot within each size class.
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Gosho, M.E. 1975. The introduction of *Mysis relicta* into freshwater lakes (a literature survey). Fisheries Research Institute circular #75-2, College of Fisheries, University of Washington.


