Feeding habits of *Mysis relicta* - an overview

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Abstract

Mysis relicta has been recognized as an important component of many limnetic food webs. The first approach to studying the feeding habits of *M. relicta* was the analysis of stomach contents. Assumptions regarding stomach content analysis have been tested and seasonal feeding estimates of *M. relicta* have been reported recently. Laboratory grazing and/ or predation experiments have recently been completed using *M. relicta* primarily from Lakes Michigan and Tahoe. *Mysis relicta* is concluded to be opportunistic, capable of utilizing a variety of food resources. It may play an important role in structuring limnetic food webs.

Introduction

Mysis relicta Lovén has long been recognized as an important component in the structure of aquatic food webs expecially as a forage for fishes. it has been reported in the stomachs of whitefish. *Coregonus clupeiformis* (Stimpson 1871); alewife, *Alosa pseudoharengus* (Stone 144); lake trout, *Salvelinus namayeush* (Hacker 1956); smelt, *Osmerus mordax* (Hale 1960); bloater, *Coregonus hoyi* (Wells & Beeton 1963); burbot, *Lota lota* (Baily 1972); fourhorned sculpin, *Myoxocephalus quadricornis* (Reynolds & DeGraeve 1972), and kokanee salmon, *Oncorhynchus nerka* (Norhcote 1973). Because of its importance in fish diets. Larkin (1948) suggested introducing *Mysis relicta* into subalpine and alpine lakes with low bottom fauna densities. Numerous lakes have received introductions of *M. relicta* since Larkin's suggestion including Kootenay Lake, British Columbia (Sparrow *et al.* 1964) and Lake Tahoe, California Nevada (Linn & Frantz 1965). Unexpected fluctuations in zooplankton community structure have occurred in both of those lakes (Zyblut 1970; Richards *et al.* 1975; Threkeld *et al.* 1980) suggesting that *Mysis* feeding is a significant factor in structuring zooplankton communities.

Feeding mechanisms

The feeding habits of *M. relicta* have been the focus of an increasing number of investigations, yet our understanding of them remains incomplete. The feeding mechanism of *M. relicta* is similar to that of *Hemimysis lamornae* which has been described in great detail by Cannon & Manton (1927). Feeding mechanisms for the Mysidacea have been reviewed by Mauchline (1980). Mysids are capable of two modes of feeding. First, they can filter-feed upon suspended particles in the feeding current. The proximal endites of the second maxillae and first thoracic endopodites contain filtering combs used in filter feeding (Grossnickle 1978).

A second feeding mode is raptorial feeding upon large masses of food. The first two thoracic endopodites hold the food while the incisor processes of the mandibles and the distal endites of the first maxillae bite into it. Food bitten off is pushed onto the spine rows and molar processes of the mandi-

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bles. After the food is ground by the molar processes it passes through the esophagus to the stomach by peristalsis.

Grossnickle (1978) compared a portion of the filter-feeding mechanism of *M. relicta* with that of *Hemimysis lamornae* reported by Cannon & Manton (1927). Both species have well-developed mandibular molar processes capable of grinding diatoms. *M. relicta* has about 16 rows of ridges on each molar process (Grossnickle 1978) and, thus, it may have a slightly larger grinding surface than *H. lamornae* which has about 13 rows of ridges (Cannon & Manton 1927). The relationship between larger molar processes and greater herbivory has been established for euphausids by Nemoto (1967). A similar relationship may exist among natural populations of Mysidacea, e.g., it appears that *M. relicta* has larger molar processes than *H. lamornae* and, thus, is capable of greater herbivory than *H. lamornae* (Grossnickle 1978).

Gut passage time

Stalberg (1933) determined the first gut passage times for *M. relicta* using a carmine suspension as a tracer. The tracer was found in the stomachs within 6–20 min after the start of the experiment. After about 2 h the entire stomach and thorax portion of the intestine contained carmine suspension. Fecal pellets were discharged 1.75 h after the start of the experiment. Stalberg reported gut passage time as rapid as 35 min, but a portion of the tracer remained in the gut of one individual for over 5.5 h. Lasenby (personal communication) has found some tracer remaining even 48 h after *M. relicta* was allowed to ingest a tracer. Therefore, gut passage time in *M. relicta* appears to be variable and may depend upon the type of particulate matter offered, the physiological state of the animal, the temperature of the medium, and possibly other physiological factors.

Stomach content analysis

The first approach to the study of the feeding habits of *Mysis relicta* was the analysis of stomach contents. Tattersall & Tattersall (1951) reported that Sars (presumably in 1867) found the remains of copepods, cladocerans, and ostracods such as *Cyclops, Bosmina,* and *Cypris* in *Mysis* guts (Table 1). Forbes (1882) found relatively few *Bosmina* in his zooplankton collections from Grand Traverse Bay, Lake Michigan; however, *Bosmina* occurred very commonly in the stomachs of *M. relicta* collected from that region. Forbes' results suggest positive selection by *Mysis* for *Bosmina.*

Stalberg (1933) found *Dinobryon* spp., *Tabellaria fenestrata* and centric diatoms in the guts of *M. relicta* collected from lake Vättern, Sweden. He also found chitin and inorganic bottom sediments in *Mysis* stomachs but plant material dominated the stomach contents. He concluded that phytoplankton was the primary food source of *M. relicta* in Lake Vättern.

Larkin (1948) suggested both herbivorous and predaceous feeding by *M. relicta* in Great Slave Lake, Northwest Territories. Tattersall & Tattersall's (1951) review of the British Mysidacea considered *M. relicta* to be primarily a detritivore.

Table 1. Pre-Rybock studies analyzing the stomach contents of *Mysis relicta.*

Author(s)	Date	Lake	Stomach contents	Conclusion(s)
Sars	1867		*Cyclops, Bosmina, Cypris*	
Forbes	1882	Michigan	*Bosmina* very common	Selection for *Bosmina*
Stalberg	1933	Vättern	*Dinobryon, Tabellaria fenestrata,* centrics, inorganic material	Phytoplankton primary food source
Green	1965	Cayuga	Cladocera, Copepoda Ostracoda, and small *Pontoporeia*	Zooplankton and benthos consumed
McWilliam	1970	Michigan	*Melosira, Tabellaria, Stephanodiscus* – all *Mysis;* algae, detritus, Cladocera, Copepoda, and small *Mysis* – large *Mysis*	'Facultative herbivores'; Selection – particle size & *Mysis* size
Lasenby & Langford	1973	Stony	Night – mostly *Daphnia*	Voracious predator at night
		Char	Mostly diatoms and inorganic material	Omnivore, primarily herbivorous

Holmquist (1959) considered *M. relicta* to be primarily a filter feeder in her review of glacial relicts of the genus *Mysis*. Thus, several hypotheses of the feeding habits of *M. relicta* had been postulated by 1959 but little evidence existed to support or refute any of them.

Green (1965) analyzed the stomach contents of *M. relicta* collected in bottom trawls in Cayuga Lake, New York. Stomach contents included fragments of cladocerans, copepods, ostracods, and small *Pontoporeia affinis* (i.e., *P. hoyi*). Green's results imply that *Mysis* can utilize both the planktonic and benthic carbon pools. Parker (1979) provided additional support for such a hypothesis. In benthic microcosms studied under laboratory conditions, *M. relicta* collected from Lake Michigan preyed upon *Pontoporeia hoyi*.

McWilliam (1970) qualitatively examined the gut contents of immature and adult *M. relicta* collected from Lake Michigan. Diatoms, including *Melosira, Tabellaria,* and *Stephanodiscus* dominated the whole or damaged plant material in the guts of all sizes of *Mysis* collected during May or June. Smaller fragments of filaments of the same diatoms were found in the stomachs of juveniles. Large immature and adult mysid stomachs contained the remains of algae, detritus, cladocerans, copepods, and small *Mysis*. McWilliam concluded that all sizes of *Mysis* were 'facultative herbivores' in Lake Michigan, and food selection was based on particle size in relation to the size of the individual.

Lasenby & Langford (1973) examined the gut contents of *M. relicta* collected from a eutrophic and oligotrophic lake. In eutrophic Stony Lake *Mysis* was a benthic detritivore by day and a voracious predator by night. In oligotrophic Char Lake *Mysis* fed primarily upon diatoms and inorganic particles on a moss substrate. They concluded that *Mysis* was omnivorous in both lakes, but primarily a nocturnal predator in Stony Lake and primarily a herbivore in Char Lake.

Lake Tahoe

Rybock (1978) developed a new approach to estimating the feeding rates of *Mysis* which is basically a modification of Petipa's (1958) method for zooplankton. He compared the stomach contents of mysids collected during ascent with those of mysids collected during descent. He called the ascending mysids the 'before' feeding group and the descending mysids the 'after' feeding group. He also calculated rates of digestion and egestion as well as feeding duration. This allowed him to calculate *in situ* feeding rates without manipulating either the mysids or their feeding medium. He also estimated a correction factor which was a ratio of the number of prey eaten to the number of prey parts in the stomach. In addition, he determined the stomach loss rate which was the number of prey parts lost from a *Mysis* stomach per hour. These corrections are often omitted from analyses of gut contents and, thus, Rybock's approach was a significant advance in the analysis of mysid stomach contents.

Rybock has also been the only investigator to analyze stomach contents at all seasons of the year. In addition, he collected the natural prey assemblage at the same time he collected the *Mysis* which allowed him to estimate selectivity.

Rybock found positive selection for *Epischura* and *Kellicottia* in L. Tahoe and for *Bosmina* in Emerald Bay, which is an isolated bay of L. Tahoe (Table 2). He also found a consistently negative selection for *Diaptomus*. Mean predation rates were correlated with prey density. Prey density was low during fall, winter, and early spring, high during late spring and early summer, and decreasing in late summer to fall values. Rybock found no size selection during fall and winter, but he found strong size selection for larger individuals during summer. Lake Tahoe juveniles ate mostly *Kellicottia,* diatoms, and detritus. A doubling in *Mysis* size resulted in an 8–10 fold increase in feeding rates. Also, *Mysis* becomes essentially a predator in Lake Tahoe at 7–8 mm.

Mean predation rates for large *Mysis* (i.e., more than 18 mm) illustrate their voracious potential in Lake Tahoe. Rybock (1978) reported 1.72 *Epischura nevadensis,* 0.44 *Diaptomus tyrelli,* and 3.53 *Kellicottia longispina* eaten per *Mysis* per hour in an 8.2 h experiment on 6 June 1978 at his index station in Lake Tahoe.

In a laboratory study of *Mysis* feeding habits in Lake Tahoe, Cooper & Goldman (1980) found that clearance rates or k values (Dodson 1975) were not affected by changes in prey density or *Mysis* density when only one type of prey was offered. In two-prey systems k values for *Epischura* were twice those for *Diaptomus*. In their assemblage experiments the

Table 2. Field and laboratory studies of the feeding habits of *Mysis relicta* in Lake Tahoe.

Author(s)	Date	Approach	Results/conclusions
Rybock	1978	1. Compared stomach contents of *Mysis* collected during ascent vs. those collected during descent 2. Prey assemblage collected with *Mysis* allowed calculation of electivities	1. Positive selection for *Epischura Kellicottia,* and *Bosmina* 2. Negative selection for *Diaptomus* 3. Predation rates correlated with prey density – low during fall-early spring, high during late spring-early summer 4. No size selection during fall or winter, but strong selection for larger prey in summer 5. Juveniles eat mostly *Kellicottia,* diatoms, and detritus. 6. A doubling in *Mysis* length results in 8–10 fold increase in clearance rates 7. *Mysis* becomes a predator at 7–8 mm
Cooper & Goldman	1980	1. Lab predation experiments using single-prey, two-prey, and multiple-prey systems.	1. Clearance rates (k) not affected by changes in prey or *Mysis* density for any single-prey system 2. In two-prey system k values for *Epischura* twice those for *Diaptomus* 3. Using natural prey assemblages smallest *Mysis* preferred smallest prey *(Bosmina, Ceriodaphnia, Diaptomus* nauplii), larger *Mysis* preferred larger prey *(Epischura, Daphnia)* 4. Total clearance rates increased with increasing mysid size and longer starvation prior to experiment 5. Food selection dependent upon mechanical efficiency of *Mysis,* vigor of prey escape responses, and food availability

Table 3. Field and laboratory studies of the feeding habits of *Mysis relicta* in Lake Michigan.

Author(s)	Date	Approach	Results/conclusions
Grossnickle	1978	1. Lab grazing experiments based upon changes in chlorophyll *a* for three size fractions of natural phytoplankton assemblage 2. Lab predation experiments using single- and two-prey systems 3. Lab grazing and predation experiments	1. Significant clearance rates upon the largest size fraction 2. In either single-prey or two-prey experiments, k values declined in sequence: *Daphnia, Cyclops, Diaptomus, Limnocalanus* 3. *Mysis* omnivorous – significant grazing and predation
Bowers & Grossnickle	1978	1. Lab grazing experiments using only large size fraction 2. Field monitoring of vertical migration and vertical chlorophyll profile	1. Significant clearance rates upon large size fraction 2. Small but significant increase in small size fraction – fragments from large size fraction increasing small size fraction 3. *Mysis* migrates into chlorophyll *a* maximum in thermocline
Grossnickle	1979	1. Fluorometric analysis of gut contents during ascent, 3 h, and 6 h later	1. Significant increase in phaeopigments within 3 h after ascent 2. All *Mysis* filter feed on phytoplankton during summer diel vertical migrations

smaller mysids preferred smaller prey such as *Bosmina, Ceriodaphnia,* or *Diaptomus* nauplii whereas the larger *Mysis* preferred larger prey such as *Epischura* or *Daphnia.* Total clearance rates increased with increasing mysid size and longer starvation prior to the experiment. Finally, food selection was dependent upon three factors: first, the mechanical efficiency of *Mysis* to capture its food; second, the vigor of the prey escape response; and third, the availability of food items. Both of these Lake Tahoe studies noted the paucity of large phytoplankton as a food source for *Mysis* in Lake Tahoe.

Lake Michigan

In contrast to the conclusions from Lake Tahoe, Grossnickle (1978) found that herbivory may comprise a significant portion of the diet of Lake Michigan mysids (Table 3). He estimated grazing rates by measuring the change in chlorophyll *a* concentrations for three size fractions of the natural phytoplankton assemblage. Predation experiments were also conducted using either one or two prey. In addition, grazing and predation rates were both estimated in the same experiment.

When offered the natural Lake Michigan phytoplankton assemblage, juvenile and adult female *M. relicta* fed predominantly upon the largest size fraction (>53 μm) with smaller clearance and ingestion rates in the middle size fraction (10–53 μm) (Grossnickle 1978). Instar I, Instar II, and adult female clearance rates were not significant upon the smallest size fraction (<10 μm) in any of his ten grazing experiments using the natural phytoplankton assemblage. Adult female clearance rates were significant only in the largest size fraction (Grossnickle 1978; Bowers & Grossnickle 1978).

Grossnickle (1978) consistently observed larger chlorophyll concentrations in the smallest size fraction in the experimental chambers (with *Mysis*) than in the control chambers (without *Mysis*). This prompted Bowers & Grossnickle (1978) to offer only the largest size fraction to *Mysis* to test if fragmentation occurred. When offered only the largest phytoplankton resuspended in filtered lake water, *Mysis* fragmented the material and the fragments were observed as significant increases in the smallest size fraction. Thus, the mysids may be increasing the potential food resources of zooplankton such as *Diaptomus ashlandi* which filter feed only upon the smallest size fraction (Bowers & Grossnickle 1978).

In 4-hour laboratory predation experiments using single-prey systems, Grossnickle (1978) reported *ca.* 1.5 up to 5 *Diaptomus* spp. or *ca.* 2.5 up to 7 *Cyclops bicuspidatus thomasi* eaten per adult *Mysis* per hour for initial prey densities of 25, 50, or 100 prey per liter. These predation rates are of the same magnitude as Rybock (1978) reported for Lake Tahoe. Thus, Lake Michigan and Lake Tahoe *Mysis* are potentially voracious predators upon copepods and other zooplankton.

In laboratory predation experiments using single-prey or two-prey systems, Grossnickle (1978) reported that clearance rates decreased in the following sequence: *Daphia, Cyclops, Diaptomus,* and *Limnocalanus.* Low clearance rates upon *Limnocalanus* were suggested to be the result of a rapid escape response. Adult female mysids were omnivorous when both the natural phytoplankton assemblage and one or two prey species were offered. That is, clearance rates were significant upon both phytoplankton and zooplankton (Grossnickle 1978).

The relationship between the vertical migratory behavior of *M. relicta* and the vertical structure of phytoplankton biomass was investigated by Bowers & Grossnickle (1978). Using a high-frequency echosounder they found a dense band of *Mysis* occurring within the subsurface chlorophyll *a* maximum. The largest size fraction of phytoplankton (i.e., the primary phytoplankton food resource available for *M. relicta*) dominated the chlorophyll *a* maximum located in the thermocline or upper hypolimnion. Thus, *M. relicta* may feed upon large phytoplankton during their summer diel vertical migrations into a subsurface chlorophyll *a* maximum in Lake Michigan (Bowers & Grossnickle 1978).

Grossnickle's (1979) investigation provides more direct evidence coupling the vertical migratory behavior of *M. relicta* with filter feeding upon phytoplankton in Lake Michigan. Using a modification of Mackas & Bohrer's (1976) method, he determined gut fullness by analyzing gut contents fluorometrically. Mysids collected during ascent, three, and six hours later were compared.

Grossnickle (1979) found a significant increase in gut phaeopigments within 3 h after after ascent. This increase occurred for all size classes of *Mysis* on all sampling dates. Changes in gut phaeopigments between ascent and 6 h later occurred in 11 of 12 comparisons (P = 0.05). Grossnickle concluded that all size classes of *Mysis* filter feed upon phytoplankton during their summer diel vertical migrations in Lake Michigan.

Other studies

The feeding behavior of *M. relicta* collected from Lake Michigan was studied in the laboratory by DeGraeve & Reynolds (1975). They reported mysids moving up to 5 cm horizontally in rapid, jerking movements to capture food particles or brine shrimp drifting downward. They suggested that cannibalism by adult mysids upon young was common in captivity.

Recent studies reported elsewhere in this volume support and confirm the conclusion that *M. relicta* is an opportunistic omnivore.

Conclusion

The feeding appendages of *Mysis relicta* are capable of both filter-feeding and raptorial feeding modes. Stomach content analysis and laboratory feeding experiments suggest that feeding is limited by the efficiency of the feeding mechanism, by the vigor of the prey escape response, and by the availability of food. *Mysis relicta* is an opportunistic omnivore. It is capable of utilizing the relatively high concentrations of diatoms and other large plankton in Lake Michigan. In lakes with relatively low concentrations of large phytoplankton (e.g., Lake Tahoe), *M. relicta* can switch to an almost exclusively raptorial feeding mode. *Mysis relicta* can utilize plankton, benthos, and probably detrital carbon pools; thus, it may play an important role in the structuring of some limnetic food webs.

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