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Predation by longfin smelt (*Spirinchus thaleichthys*) on the mysid *Neomysis mercedis* in Lake Washington

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SUMMARY

1. Longfin smelt and mysid samples collected in Lake Washington from 1988 to 1992 were examined, and historic data on smelt and mysid abundance were reviewed to assess the impacts of smelt predation on *Neomysis mercedis*. The feeding habits of smelt were also examined for differences between odd and even years, and seasonal and ontogenetic variations in smelt diet were described.
2. A reciprocal relationship in the abundance of 1+ smelt and *Neomysis* suggested that smelt regulate mysid abundance in the lake.
3. The proportion of smelt diet contributed by mysids was higher for less abundant year classes of smelt.
4. These results indicate that intraspecific competition for scarce mysids occurs in the even-year classes of smelt.

Introduction

Several studies have demonstrated that planktivorous fish can alter zooplankton abundance and species composition in lacustrine ecosystems (Brooks & Dodson, 1965; Post & Mcqueen, 1987; Siegfried, 1987). However, few studies have shown that predation by fish could also affect mysid abundance. Siegfried (1987) noted that the abundance and biomass of *Mysis relicta* Loven were lower in the south basin of Lake George, New York following the establishment of large populations of rainbow smelt (*Osmerus mordax* Mitchill) than in the north basin where smelt were not abundant. McDonald, Crowder & Brandt, 1990) concluded that the decline in the density of *Mysis relicta* and an amphipod, *Pontoporeia hoyi* Smith, in Lake Michigan was as a result of an increase in the abundance of benthic-feeding fish. Kjellberg, Hessen & Nilssen (1991) observed differences between year classes in the production of *M. relicta* in Lake Mjosa, Norway and attributed this to a combination of predation by smelt (*O. eperlanus* L.) and food availability.

In Lake Washington (Seattle, WA, U.S.A.) longfin smelt (*Spirinchus thaleichthys* Ayres) is an important part of the planktivore assemblage. They mature at the end of two years, after which the majority, if not all, spawn and die. Spawning occurs mainly in the Cedar river (which flows into the south end of the lake) during winter/early spring (Moulton, 1974). By July, young of the year (YoY) smelt are easily captured in the limnetic area of the lake. In the 1960s, longfin smelt were reported to have fed mainly on mysids (Dryfoos, 1965), although the number of mysids observed in individual smelt stomachs in recent times has decreased (Chigbu & Sibley, 1994a). During the late 1960s, smelt abundance increased in the lake (Moulton, 1974) and the population abundance of *Neomysis mercedis* Holmes declined. Moulton (1970) and Edmondson & Abella (1988) hypothesized that predation by smelt was responsible for the observed change in mysid density. An unusual feature of smelt populations in Lake Washington is a regular fluctuation in abundance of even- and odd-year classes. Even-year classes have been 5–15 times more abundant than odd-year classes (Beauchamp, 1987) since 1964 and 1965 when smelt were first studied in Lake Washing-

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ton (Dryfoos, 1965). Furthermore, the abundance of the even-year classes of smelt has increased recently, while the abundance of the odd-year classes has remained relatively low (Eggers *et al*., 1978; Chigbu & Sibley, 1994b). Because smelt is the most abundant planktivorous fish in Lake Washington, differences in population density between years are expected to have observable impacts on lower trophic levels.

The objectives of this study were:

1 To assess the impacts of smelt predation on *Neomysis mercedis* by comparing mysid abundance during odd years and even years. Yearling smelt are the major predators on mysids (Dryfoos, 1965; Chigbu & Sibley, 1994a). If smelt predation is the controlling factor for mysid abundance, population density should be reduced during odd years when 1+ smelt are abundant.

2 To compare the overall feeding habits of smelt between odd years and even years.

3 To describe seasonal and ontogenetic variations in smelt diet.

Materials and methods

Sample collection

From November 1988 to February 1992, sampling was conducted in Lake Washington using a 3-m Isaacs–Kidd midwater trawl (Isaacs & Kidd, 1953) with a 7.68 m^2 cross-sectional area (Traynor, 1973). The trawl has three sections: a forward section made of 3.2-cm stretch mesh; an intermediate section of 3.2-cm stretch mesh separated by 62-cm-diameter rings; and a cod-end made of a 5-mm knotless nylon.

Trawling always commenced shortly after dusk because longfin smelt and mysids disperse in the water column at night and feed intensely during that time (Dryfoos, 1965; Eggers *et al*., 1978). Trawling was conducted at pre-selected depths between 8 m and 50 m in five areas of the lake using the research vessel, Clifford Barnes. Each trawl was maintained for 10 min at about 5 knots. After each trawl, the net was well rinsed into a plastic tub and all captured fish were identified to species and counted. Mysids were captured by passing the rinse water through a 12-inch sieve with a 5-mm mesh size. All smelt and mysids caught were counted and preserved in 10% formalin.

Estimation of smelt and mysid abundance

1+ smelt were separated from YoY smelt by length frequency analysis. Information on the spawning period and duration of egg development of smelt is available (Dryfoos, 1965; Moulton, 1974), so it was possible also to estimate the ages (in months) of the fish (Chigbu & Sibley, 1994b). Smelt (1+) and mysid abundances are expressed as mean catch per effort (CPUE) and are used as indices of abundance. The total number of 1+ smelt or mysids caught during a two-night survey was divided by the total number of trawls (usually twenty-five) to calculate mean CPUE. Then, using each trawl as a replicate, CPUE of 1+ smelt and mysids were compared between odd and even years.

Historic data on smelt and mysid abundance

Long-term data on the annual mean density of mysids from 1963 to 1992 (Murtaugh, 1981; A. H. Litt and W. T. Edmondson, unpublished data) and data on 1+ smelt abundance were examined by consulting reports prepared by the Fisheries Research Institute, University of Washington, Seattle and the Washington State Department of Fisheries (see Chigbu & Sibley, 1994b). Thereafter, the relationship between annual mean density of mysids and 1+ smelt was assessed.

Examination of stomach content of smelt, and conversion of prey numbers into dry weight

Fish from each year class (YC) were selected, measured to the nearest 1.0 mm and weighed to the nearest 0.01 g, in the laboratory (Table 1). The stomachs of individual fish were slit open and their contents emptied into a Petri dish, identified and counted under a dissecting microscope. Data were recorded as numbers of individuals in each prey taxon.

Intact *Daphnia* observed in the stomachs of individual fish were measured from the anterior margin of the head to the base of the tail spine. Mysid telson length was also measured. The numbers of *Daphnia* counted were converted into dry weights using a length (mm)–weight (μg) regression relationship for *Daphnia* species from Lake Washington established by Chigbu (1993):

Table 1 Summary of smelt samples by month and year

	Fish examined (n)	Fish with gut contents (n)	Mean S.L. ± SE (mm)	Range (mm)
1988 YC				
YoY Smelt, Nov. 1988	8	7	50.13 ± 2.99	37–63
1+ Smelt, July 1989	78	66	80.76 ± 1.28	63–106
1+ Smelt, Dec. 1989	10	9	85.00 ± 3.43	71–103
1+ Smelt, Jan. 1990	14	13	93.64 ± 2.04	75–107
1989 YC				
YoY Smelt, Dec. 1989	4	3	40.50 ± 2.72	36–48
1+ Smelt, May 1990	10	5	89.80 ± 2.22	75–98
1+ Smelt, July 1990	62	51	95.71 ± 0.89	78–107
1+ Smelt, Nov. 1990	9	7	102.44 ± 1.43	98–109
1+ Smelt, Feb. 1991	5	5	112.60 ± 2.66	108–122
1990 YC				
YoY Smelt, July 1990	19	14	29.10 ± 0.94	22–35
YoY Smelt, Sep. 1990	17	16	37.00 ± 1.65	32–45
YoY Smelt, Nov. 1990	5	5	49.71 ± 2.54	38–59
YoY Smelt, Feb. 1991	8	5	66.50 ± 2.28	57–75
1+ Smelt, May 1991	10	9	59.30 ± 1.67	53–70
1+ Smelt, Jun. 1991	10	10	71.30 ± 2.05	63–85
1+ Smelt, Oct. 1991	10	9	82.60 ± 1.98	73–90
1+ Smelt, Dec. 1991	10	10	81.90 ± 1.93	72–92

S.L., standard length; YC, year class; YoY, young of the year; 1+, 1 year and older

$\text{Ln}\ (Wt) = 0.94 + 2.23\ \text{Ln}\ (L)$
$P < 0.05,\ r^2 = 0.765,\ n = 415.$

Similarly, the numbers of mysids were converted into dry weights using the following length (mm) –dry weight (mg) regression equation (Chigbu & Sibley, 1996):

$\text{Ln}\ (Wt) = -5.02 + 2.57{*}\text{Ln}\ (L)$
$P < 0.0001,\ r^2 = 0.960,\ n = 63$

where L = total length (from the apex of the rostrum to the posterior margin of the telson). For other prey species, numbers were converted to dry weights using monthly mean dry weight values determined by Doble & Eggers (1978).

Results

Abundance of 1+ smelt and mysids in Lake Washington

The abundance of 1+ smelt and mysids in various seasons and years are presented in Fig. 1. A comparison of 1+ smelt abundance between even and odd years using a Mann–Whitney *U*-test, showed that median CPUE of 1+ smelt was higher in July ($P = 0.09$), December ($P < 0.001$) and May ($P > 0.05$) in odd years than in even years. In February, 1+ smelt median CPUE was higher during even years ($P < 0.001$) than during the corresponding month in odd years.

Mysid median CPUE was higher during July ($P < 0.01$), November ($P < 0.05$) and May ($P = 0.09$) of even years than odd years except in February ($P = 0.09$) when median CPUE was higher in odd years than in even years (Fig. 1). When summer and autumn data were pooled, it was observed that CPUE of mysids was significantly higher (Kruskal–Wallis, $P < 0.001$) in 1990 (mean = 175.41 ± 27.27 SE, $n = 49$) than in 1989 (mean = 99.77 ± 22.48 SE, $n = 48$) or 1991 (mean = 31.72 ± 2.97 SE, $n = 67$).

Historic data on *Neomysis* abundance in the lake were examined to evaluate whether mysid abundance is lower during odd years, when 1+ smelt abundance is high, than even years. From 1963 to 1983, mysid abundance was not consistently higher in even years than in odd years (Fig. 2a), but, from 1984 to 1992, mysid data suggest that odd-year abundances were always lower than those in even years (Fig. 2b). As a

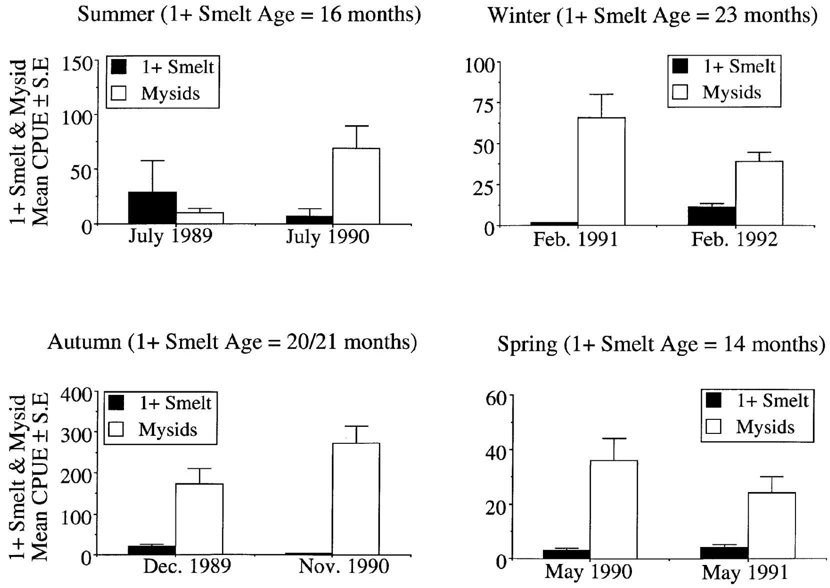

Fig. 1 Variations in the mean catch per effort (CPUE) of 1+ smelt and *Neomysis mercedis* Holmes during odd and even years. Median CPUE for 1+ smelt differed significantly between odd and even years in autumn and winter ($P < 0.001$) but not in summer ($P = 0.09$) and spring ($P > 0.05$). Median CPUE for *N. mercedis* differed significantly between odd and even years in summer and autumn ($P < 0.05$) but not in spring and winter ($P = 0.09$).

result, there was an inverse relationship between 1+ smelt and mysid abundances (Fig. 2c).

Differences between diet of even- and odd-year classes of smelt

Diet of 1988–1990 year classes of smelt expressed as percentage dry weight are presented in Fig. 3. Four prey types, mysids, *Epischura*, amphipods and *Daphnia*, comprised 50% or more of the dry weight of prey. The proportion of the dry weight of diet contributed by mysids was generally higher for the 1989 year class than the 1988 or 1990 year classes; for example, from summer to winter, mean contributions of mysids to 1+ smelt diet were 53.03% and 82.93% for the 1988 and 1989 year classes, respectively. Moreover, the mean percentage frequency of occurrence of mysids in 1+ smelt stomachs was about three times higher in the 1989 (60.40%) than in the 1988 year class (21.83%) during the same period. When data collected during summer and autumn were averaged, mysid contributions in dry weight were 58% for the 1988, 74% for the 1989 and 37% for the 1990 year class.

During autumn, diet of 1988 year class smelt (YoY) comprised higher amounts of *Daphnia* (50%) than diet of 1989 (1.2%) or 1990 year classes (26%). In contrast, *Epischura* was more important in 1989 year class diet (93%) than 1988 or 1990 year classes (Fig. 3). Similarly, 80–100% of the even-year class smelt examined consumed *Daphnia*, whereas only 33% of the odd-year class fish ingested *Daphnia*.

In winter, about 49% of 1988 year class (1+ smelt) diet was amphipods; none was observed in stomachs of the 1989 year class (1+ smelt).

Seasonal, ontogenetic shift in the diet of smelt

1988 year class. The diet of 1988 year class fish, expressed as percentage dry weight, changed significantly between November 1988 and January 1990 (Fig. 3). In November 1988, YoY smelt diet was composed primarily of *Daphnia* (50%) and chironomid larvae (33%); *Leptodora* (5%) and copepod species (0.6–7.2%) were consumed but not in large amounts. In July, mysids (26%), chironomids (13%), *Leptodora* (13%), fish (10%), and *Daphnia* (29%) were the main components of 1+ smelt diet. Copepod species were of little importance. Mysids were the most important prey in December 1989 for 1+ smelt, followed by chironomid larvae (5%). In January 1990, mysids (43%) and amphipods (49%) were almost of equal importance. Generally, as the 1988 year class smelt grew, their diet from November 1988 to January 1990 was characterized by: (i) an increase in mysid contribution; (ii) an increase in the proportion of amphipods; and (iii) a decrease in the proportion of chironomids, *Diaptomus*, *Leptodora* and *Daphnia*. The diet of 1988 year class smelt expressed in terms of frequency of occurrence is contained in Table 2. In November 1988, *Daphnia* were observed in virtually all smelt. Although copepod species were of minor importance in smelt diet on a dry weight basis (Fig. 3),

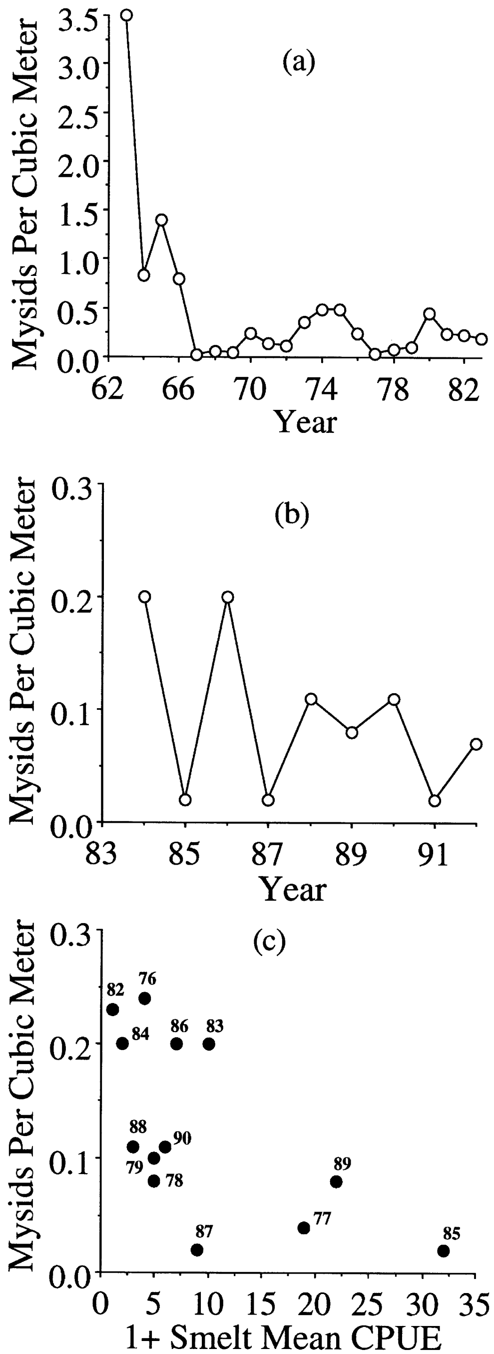

Fig. 2 (a) Annual mean density of mysids in Lake Washington (1963–83). Data are from Murtaugh (1981), and A. H. Litt and W. T. Edmondson (unpublished). (b) Annual mean density of mysids in Lake Washington (1984–92). Data are from samples provided by A. H. Litt and W. T. Edmondson. (c) Relationship between annual mean density of *Neomysis mercedis* and 1+ smelt mean CPUE collected in various years. Smelt samples were collected in March/April. Data are from Fisheries Research Institute, University of Washington reports and Washington Department of Fisheries (see Chigbu & Sibley, 1994b).

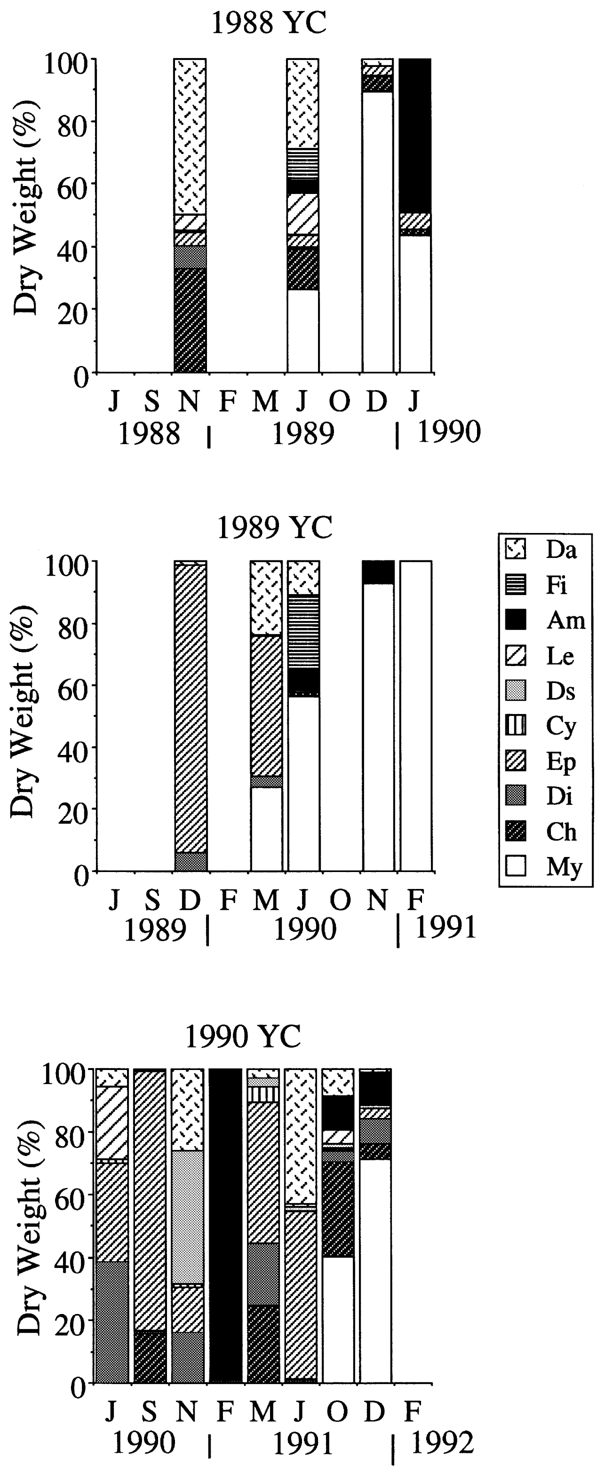

Fig. 3 Monthly and yearly variations in smelt diet (% dry weight). ***Da***, *Daphnia* spp.; ***Fi***, fish larvae; ***Am***, amphipods; ***Le***, *Leptodora kindtii* Focke; ***Ds***, *Diaphanosoma*; ***Cy***, *Cyclops bicuspidatus thomasi* S.A. Forbes; ***Ep***, *Epischura nevadensis* Lilljeborg; ***Di***, *Diaptomus ashlandi* Marsh; ***Ch***, Chironomid larvae; ***My***, *Neomysis mercedis* Holmes.

more than 50% of the fish consumed copepod species. In July and December 1989, more smelt consumed *Daphnia* (89%) than any other prey. In January 1990, 92% of fish consumed amphipods. Fewer fish fed on the other prey species.

1989 year class. The relative importance of large prey such as mysids and amphipods increased as smelt grew from a mean size of 41 mm in December 1989 to 113 mm in February 1991, whereas the importance of small prey such as copepod species and *Daphnia* decreased (Fig. 3). In December 1989, 0+ smelt diet was dominated by *Epischura* (93%). Mysids were not observed and *Daphnia* (1%) were negligible. *Epischura* also dominated the diet of 1+ smelt in May 1990 (40%), although mysids (27%) and *Daphnia* (24%) importance had increased. In decreasing order of importance, mysids (56%), fish (24%) and *Daphnia* (11%) were the major prey of 1+ smelt in July 1990. Adult smelt fed almost entirely on mysids in November 1990 (93%) and February 1991 (99.9%). The percentages of 1989 year class fish that consumed various prey types are shown in Table 2. *Epischura* was the most prevalent in December 1989 for 0+ smelt. By May 1990, *Daphnia* (100%), *Diaptomus* (80%) and *Cyclops* (80%) had become the most commonly consumed prey. *Daphnia* (88%) were also more common than mysids (10%) in July 1990, although in terms of biomass, mysid contribution was greater than that of *Daphnia* (Fig. 3). In November 1990, about 71% of 1+ smelt consumed mysids or *Daphnia*, whereas in February 1991 all 1+ smelt examined contained mysids in their stomachs.

1990 year class. The most complete set of feeding information was collected for the 1990 year class (Fig. 3). Mean size of fish examined increased from 29 mm in July 1990 to 82 mm in December 1991 (Table 1). The dominant prey in July 1990 for 0+ smelt were *Diaptomus* (39%), *Epischura* (31%) and *Leptodora* (22%). In September 1990, 0+ smelt fed primarily on *Epischura* (83%), but *Diaphanosoma* (42%) and *Daphnia* (26%) were more important in November 1990 than *Diaptomus* (16%) or *Epischura* (14%).

In February 1991, 0+ smelt consumed essentially amphipods (99%). Three prey types, chironomids (25%), *Diaptomus* (20%) and *Epischura* (45%) comprised about 90% of 1+ smelt diet in May 1991, but in June 1991 1+ smelt fed mostly on *Epischura* (53%) and *Daphnia* (42%). Large prey such as mysids (40%), chironomids (30%) and amphipods (11%) dominated 1+ smelt diet in October 1991, although *Daphnia* (9%) were also consumed. In December 1991 1+ smelt fed little on *Daphnia* (1%) but concentrated on mysids (71%) and amphipods (10%).

Although mysids and chironomids were a significant component of smelt diet on the basis of prey biomass (Fig. 3), they were not observed in more than 25% of the fish during any month (Table 2). This was also true for amphipods, except in February 1991 when 80% of all 0+ smelt examined contained amphipods. *Diaptomus*, *Epischura* and *Daphnia* were quite common in 1990 year class smelt, especially from November 1990 to December 1991.

Discussion

Generally, on sampling occasions in odd years, 1+ smelt CPUE were higher than in even years, whereas the reverse was the case for mysids. Mysid life history information presented by Murtaugh (1983); Murtaugh (1989) agrees with the observation of the present study that mysid density in Lake Washington is higher during even than odd years; for example, the mean cohort density (gravid females) in autumn 1980 was about one and a half times higher than in autumn 1979. Similarly, mean cohort density in winter/spring 1980 was four times higher than in winter/spring 1979 (Murtaugh, 1989). Furthermore, estimates of mysid density in Lake Washington from the present study, based on samples collected with bongo nets, were higher in November 1990 (1.06 mysids m^{-3}) than in December 1991 (0.19 mysids m^{-3}) (Chigbu, 1993). This reciprocal relationship in the abundance of 1+ smelt and mysids is consistent with a high predation impact of smelt on mysids, especially during odd years. Although several years of data on smelt abundance in Lake Washington have demonstrated that 1+ smelt abundance is higher during odd years than even years (Chigbu & Sibley, 1994b), similar fluctuations have not previously been demonstrated for the mysid population in Lake Washington. The findings in this study are not only consistent with the hypothesis that longfin smelt control *Neomysis* abundance in Lake Washington, but also agree with the conclusions that: (i) the decrease in *M. relicta* abundance in various lakes was a result of predation by smelt (Siegfried, 1987; Kjellberg *et al*., 1991); and (ii)

Table 2 Monthly and yearly variations in smelt diet (% frequency of occurrence)

	My	*Ch*	*Di*	*Ep*	*Cy*	*Ds*	*Le*	*Am*	*Fi*	*Da*
1988 YC										
YoY Smelt, Nov. 1988	0.00	14.30	100.00	42.90	57.10	0.00	14.30	0.00	0.00	100.00
1+ Smelt, Jul. 1989	9.10	12.10	53.00	72.70	28.80	0.00	48.50	4.50	4.50	89.40
1+ Smelt, Dec. 1989	33.30	22.20	33.30	66.70	0.00	0.00	0.00	0.00	0.00	88.90
1+ Smelt, Jan. 1990	23.10	7.70	30.80	30.80	15.40	0.00	0.00	92.30	0.00	7.70
1989 YC										
YoY Smelt, Dec. 1989	0.00	0.00	66.60	100.00	0.00	0.00	0.00	0.00	0.00	33.30
1+ Smelt, May 1990	20.00	0.00	80.00	60.00	80.00	20.00	0.00	0.00	0.00	100.00
1+ Smelt, Jul. 1990	9.80	2.00	23.50	3.90	52.90	0.00	5.90	5.90	13.70	88.20
1+ Smelt, Nov. 1990	71.40	0.00	42.90	28.60	0.00	14.30	0.00	42.90	0.00	71.40
1+ Smelt, Feb. 1991	100.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1990 YC										
YoY Smelt, Jul. 1990	7.10	0.00	42.90	7.10	35.70	0.00	7.10	0.00	0.00	35.70
YoY Smelt, Sep. 1990	0.00	15.90	28.60	100.00	14.30	0.40	0.00	0.00	0.00	0.00
YoY Smelt, Nov. 1990	0.00	0.00	100.00	80.00	80.00	100.00	0.00	0.00	0.00	80.00
YoY Smelt, Feb. 1991	0.00	0.00	40.00	0.00	0.00	0.00	0.00	80.00	0.00	0.00
1+ Smelt, May 1991	0.00	11.10	77.80	55.60	77.80	55.60	0.00	0.00	0.00	88.90
1+ Smelt, Jun. 1991	0.00	0.00	100.00	100.00	70.00	70.00	10.00	0.00	0.00	100.00
1+ smelt, Oct. 1991	11.10	22.20	77.80	22.20	22.20	33.30	22.20	11.10	0.00	100.00
1+ Smelt, Dec. 1991	20.00	10.00	100.00	40.00	30.00	60.00	0.00	20.00	0.00	90.00

My, Neomysis mercedis Holmes; *Ch, Chironomid larvae; Di, Diaptomus ashlandi* Marsh; *Ep, Epischura nevadensis* Lilljeborg; *Cy, Cyclops bicuspidatus thomasi* S.A. Forbes; *Ds, Diaphanosoma; Le, Leptodora kindtii* Focke; *Am,* Amphipods; *Fi,* Fish larvae; *Da, Daphnia* spp.

the increase in abundance of *Neomysis integer* Leach in Lake Wolderwijd, the Netherlands, was a result of the reduction of the biomass of its predator, perch (Meijer *et al*., 1994). An important question is, why did mysids show consistent odd-/even-year variations in abundance from 1984 to 1992 but not in previous years? The authors believe this is because decreases in mysid abundance and increases in smelt abundance in the lake have produced more tightly coupled predator–prey interactions. Moreover, the difference in the abundance of even- and odd-year classes of smelt has widened recently (see Beauchamp, 1994; Chigbu & Sibley, 1994b). Beauchamp (1994) attributed this to the stocking of rainbow trout (*Oncorhynchus mykiss* Walbaum), beginning in 1981, to increase sport fishery in Lake Washington. Rainbow trout are important predators of smelt (Beauchamp, 1990, Beauchamp, 1994), and apparently produce a depensatory impact on smelt.

Prickly sculpin (*Cottus asper* Richardson) is the only other abundant fish species that feeds substantially on mysids in Lake Washington (Eggers *et al*., 1978; Rickard, 1978). Because their biomass is high, it is likely that they also contribute significantly to mysid mortality in the lake. However, sculpin have not been reported to show odd-/even-year variation in abundance comparable to that of smelt in Lake Washington. Thus, *C. asper* predation on mysids, rather than being responsible for the between-year differences in mysid abundance, may, in fact, obscure the differences caused by odd- and even-year fluctuations in smelt abundance.

It is not clear what initiated the population cycle in Lake Washington smelt (see Chigbu & Sibley, 1994b). The mechanisms for cycles reported in other fish species (e.g. Cryer, Peirson & Townsend, 1986; Hamrin & Persson, 1986; Townsend & Perrow, 1989; Perrow, Peirson & Townsend, 1990) were intraspecific, asymmetrical competition, cannibalism, or interspecific density-dependent predation. Perhaps, the cycle in smelt was initiated by one or more abiotic factors; however, mortality resulting from trout predation is higher for the odd-year class than the even-year class smelt (Beauchamp, 1994), and thus helps to maintain the cycle. In roach [*Rutilus rutilus* (L)], poor survival of the fish because of eutrophication, coupled with intraspecific competition between YoY and breeding year classes, is one important mechanism responsible for producing population cycles (Townsend & Perrow, 1989).

Associated with the fluctuations in smelt abundance is a reduction in size at maturity and fecundity of the even-year class smelt; the odd-year class fish produce higher numbers of eggs per female than the even-year class fish (Chigbu & Sibley, 1994b). These changes in growth and fecundity were caused by a decline in the density of *Neomysis*, an important prey of smelt, resulting in more intense intraspecific competition for food among fish belonging to the even-year class, than in odd-year class smelt.

Murtaugh (1983) sampled mysids with an epibenthic sled and observed peaks in mysid abundance during spring/summer when the juveniles are released into Lake Washington. These juveniles grow through the autumn season until the next winter, when they reproduce. Samples for the present study were collected with a trawl that undersampled mysids less than 7 mm in length because of the large mesh size (5 mm) at the cod-end (P. Chigbu, unpublished data). This factor is responsible for the low abundance of mysids in summer in this study compared to the autumn. However, it is not felt that the gear size selectivity affected the assessment of smelt predation impacts on mysids remarkably, because mysid CPUE was compared between odd and even years, rather than between seasons. Moreover, from late summer to winter, mysids are dominated by large-sized individuals, and mysid density estimates from bongo net samples collected in November 1990 and December 1991 (Chigbu, 1993) support the conclusions, based on the trawl data, that mysid abundance was higher during even than odd years. If size selectivity affected the assessment in the present study of smelt predation impact on mysids, it is during spring when juveniles dominate the samples (Murtaugh, 1983).

The feeding habits of smelt varied yearly, seasonally and ontogenetically. In general, mysids contributed more to the diet of the odd-year class of 1+ smelt, which is less abundant than the even-year class. The difference in the relative biomass of mysids consumed might be responsible for the much more rapid growth of the 1989 year class (see Table 1) from 41 mm in December 1989 to 113 mm in February 1991, as opposed to the 1988 year class (50–94 mm) or the 1990 year class (50–82 mm).

The ontogenetic variations in smelt diet result from a number of factors, especially seasonal differences in availability of various prey species, spatial distribution of smelt and preference for large prey as smelt grow. Moreover, the sporadic occurrence of *Leptodora* and *Diaphanosoma* and the decline of *Daphnia* abundance in the lake from 1988 to 1992 (A. H. Litt and W. T. Edmondson, personal communication) might also contribute to the differences in smelt diet.

Smelt feed on a variety of prey types, as has been noted for other smelt species (Evans & Loftus, 1987; Nellbring, 1989). The between-year differences in the proportion of mysids consumed by 1+ smelt reflects the between-year variations in smelt and, subsequently, mysid abundances in the lake. For adult smelt, alternative prey consumption is thought to occur in response to low abundance of mysids.

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