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Feeding ecology of longfin smelt (*Spirinchus thaleichthys* Ayres) in Lake Washington

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Abstract

Stomach contents of longfin smelt collected in Lake Washington, 1985–1991, were analyzed to assess feeding habits. Copepod species dominated prey biomass consumed by young of the year smelt in summer whereas *Daphnia*, chironomid larvae, and copepod species were the most important prey in fall. Diet of 1+ smelt, expressed in terms of percent dry weight, consisted mainly of mysids, amphipods, and *Daphnia*. The mean number of mysids observed in smelt stomachs in this study was about 50% lower than in the 1960s. This change in smelt diet is related to changes that have occurred in the Lake Washington watershed, and in the zooplankton composition in the lake following recovery from eutrophication; a reduction in growth of smelt accompanied this.

Keywords: Diet; Mysids; Osmeridae; Feeding preferences; *Daphnia*

1. Introduction

A number of studies has described the feeding habits of smelt in the genus *Osmerus* (Strelnikova and Ivanova, 1982; Stedman and Argyle, 1985; Brandt and Madon, 1986; Naesje et al., 1987; Nellbring, 1989). Food organisms reported in their diet include phytoplankton, rotifers, crustacean zooplankton, amphipods, and fish (Evans and Loftus, 1987). Other studies have examined the effects of smelt feeding on aquatic communities. Reif and Tappa (1966) reported a replacement of large *Daphnia pulex* by the smaller *D. dubia* and a scarcity of *Leptodora kindtii* in Harvey Lake, Pennsylvania following introductions of rainbow smelt (*O. mordax* Mitchill). Siegfried (1987) observed that rainbow smelt selectively preyed on large-sized crustacea resulting in a change of the phytoplankton community composition in Lake George, New York. In Tjenkemeer Lake, Netherlands, *O. eperlanus* (L.) fed preferentially on *D. hyalina* thereby altering the size composition to predominantly smaller individuals. This caused a shift in the feeding behavior of bream (*Abramis brama* L.) from planktivory to benthivory, consequently affecting, adversely, the condition of mature bream (Lammens et al., 1985).

The feeding habits of longfin smelt (*Spirinchus thaleichthys* Ayres) are less well studied. In North America, the only study that examined diet of a land-locked population was conducted by Dryfoos (1965) in Lake Washington. When that investigation was

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conducted, smelt population abundance was low and mysids (*Neomysis mercedis*), which were very abundant in the lake, were the principal prey. From first summer to second winter (when smelt matured, spawned and died), mysids contributed 38.5–93.2% of smelt diet in terms of dry weight. However, mysid density declined remarkably from the early 1960s, and has remained low (Moulton, 1974; Eggers et al., 1978; Murtaugh, 1981a). In contrast, smelt abundance has increased over the years (Chigbu and Sibley, 1994a).

Because of their potential to affect other fish species adversely by reducing the abundance of large cladoceran species, preferred prey species, or by direct predation on juvenile fish, we studied the feeding response of longfin smelt to reduced abundance of mysids in Lake Washington. There are a number of possible responses, including smelt: (1) continue to feed primarily on mysids despite the substantial decline in mysid abundance with a consequent decrease in smelt body size and population abundance; (2) become more piscivorous, consuming such prey as juvenile sockeye salmon (*Oncorhynchus nerka* Walbaum); or (3) shift their diet to encompass a variety of prey. To assess whether a shift in the diet has occurred, we examined stomach contents and size of smelt collected in Lake Washington, 1985–1991, and compared the data with those of Dryfoos (1965). Information on response of fish populations to environmental change is important for management and conservation of fish species. In a previous paper, we compared diet and growth of smelt and juvenile salmon (Chigbu and Sibley, 1994b). Here we present detailed information on seasonal and ontogenetic variations in the feeding habits of smelt.

2. Materials and methods

2.1. Fish collection

Pelagic smelt and mysids were captured in Lake Washington using a 3 m Isaacs–Kidd mid water trawl, IKMT (Isaacs and Kidd, 1953). Sampling usually began soon after sunset (about an hour); the greatest feeding intensity of smelt occurs twilight to mid-night (Dryfoos, 1965). Fish were counted in the field and preserved in 10% formalin. All fish collected were measured to the nearest 1.0 mm and weighted to the nearest 0.01 g. Mysid telson lengths were also measured.

2.2. Examination of gut contents

Fish from each year class, identified by length frequency distribution, were selected and gut contents removed in the laboratory. From 1985 to 1987 whole guts of individual fish were slit open; and the contents emptied into a Petri dish, identified, and counted under a dissecting microscope. For fish collected from 1988 to 1991, only stomach contents were examined since Dryfoos (1965) examined only the stomachs of smelt.

2.3. Measurement of prey length and conversion of prey numbers into dry weight

Intact *Daphnia* observed in the gut of individual fish were measured from the anterior margin of the head to the base of the tail spine. The telson length of mysids was also measured. The numbers of *Daphnia* counted were converted into dry weights using a length (mm)–weight (ug) relationship (P. Chigbu, unpublished data) determined for *Daphnia* species:

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

For other prey species, the number of prey was multiplied by the respective mean dry weight values obtained by Dryfoos (1965) using prey species captured in September. Hence, the values do not reflect the seasonal variation in the dry weight of the prey species or changes that may have occurred since 1965. However, since an important objective of this study was to determine if the seasonal pattern of smelt feeding at present is different from that reported by Dryfoos (1965), we considered it necessary to use comparable procedures for analyzing the stomach contents.

2.4. Analysis of diet data and determination of diet breadth

Data collected in various years were pooled to determine if smelt diets today differ from the 1960s (Dryfoos, 1965). Stomach data are presented as percent frequency of occurrence (based on the number of fish with food) and percent dry weight. To evaluate seasonal differences in diet, we considered that winter=January–March, spring=April–June, summer=July–September, and fall=October–December, sensu Dryfoos (1965).

To examine changes in diet breadth of smelt since the 1960s, we used the Shannon–Weaver diversity index (Zar, 1984):

$$H' = -\sum_{j}^{r} P_j \log P_j,$$

where P_j=percent that j prey contributes to predator diet, and r=number of prey taxa utilized by predator.

The magnitude of this index depends on the number of prey taxa used by the predator. Hence, we have also calculated evenness index (relative diversity) which is expressed as

$$J' = H'/H'_{\max},$$

where $H'_{\max}$=log r.

3. Results

General information about smelt used for stomach content analysis is presented in Table 1 including: (a) months and years during which smelt stomachs were examined, (b) number of fish stomachs examined, (c) number and percent of fish with food, and (d) the size of smelt examined. Smelt fed on a variety of prey and prey diversity increased as the fish grew.

3.1. Food of young of the year (0+ group) smelt compared to the diet in 1960s

Six types of prey: chironomid larvae and pupae, copepod species such as *Diaptomus ashlandi*, *Epischura nevadensis*, and *Cyclops bicuspidatus thomasi* and the cladocerans, *Diaphanosoma leuchtenbergianum* and *Daphnia* were identified in smelt stomachs during their first summer in Lake Washington. *Epischura* occurred most frequently in the diet, followed by *Diaptomus* (Fig. 1). In terms of dry weight, copepod species were most important in YoY smelt diet (85.7%) followed by chironomid larvae (11.2%). *Epischura* (84.4%) accounted for most of the copepod weight. *Daphnia* occurred in trace amounts.

By fall, *Daphnia* species appeared in more than 80% of the fish examined. Frequency of occurrence for copepod species ranged from 50% to 100% of the stomachs (Fig. 1). Other prey species were eaten by a relatively small percentage of the fish, 40% for *Diaphanosoma* and <20% for *Leptodora* and chironomid larvae. Although chironomid larvae were present in less than 10% of the fish, they contributed about 25% of the dry weight of stomach contents. *Daphnia* were the most important crustacean prey (50%) by weight and *Cyclops* were the least important (<1%). The dry weight of *Diaptomus* and *Epischura* were about 10% and 8%, respectively.

In summer and fall, during the study by Dryfoos (1965), about 10% and 32% of YoY smelt, respectively, consumed mysids, and mysids comprised about 38–77% of prey dry weight observed in the stomachs (Fig. 2).

3.2. Food of yearling and older smelt compared to the diet in 1960s

No food item occurred in more than 50% of the fish during first and second winter. However, large prey such as mysids and amphipods were prevalent and dominated the prey biomass (Fig. 3). Amphipod bio-

Table 1
Summary of smelt samples by season and year

		Number of fish examined	Number of fish with diet (%)	Mean SL± SE (mm)	Range (mm)
YoY Smelt	Summer (September 1990)	17	16 (94.12)	36.41±1.06	29–45
YoY Smelt	Fall (November 1988 and November 1990)	13	12 (92.30)	49.54±2.19	37–63
1+ Smelt	Winter (March 1985, January 1990 and February 1991)	29	28 (96.55)	87.85±2.99	54–107
1+ Smelt	Spring (April and June 1985, April 1990)	170	145 (85.29)	70.44±1.35	41–130
1+ Smelt	Summer (July and September 1987, July 1989 and 1990)	273	242 (88.64)	85.87±0.64	63–140
1+ Smelt	Fall (November 1987 and 1988)	181	172 (95.03)	91.40±0.83	65–127

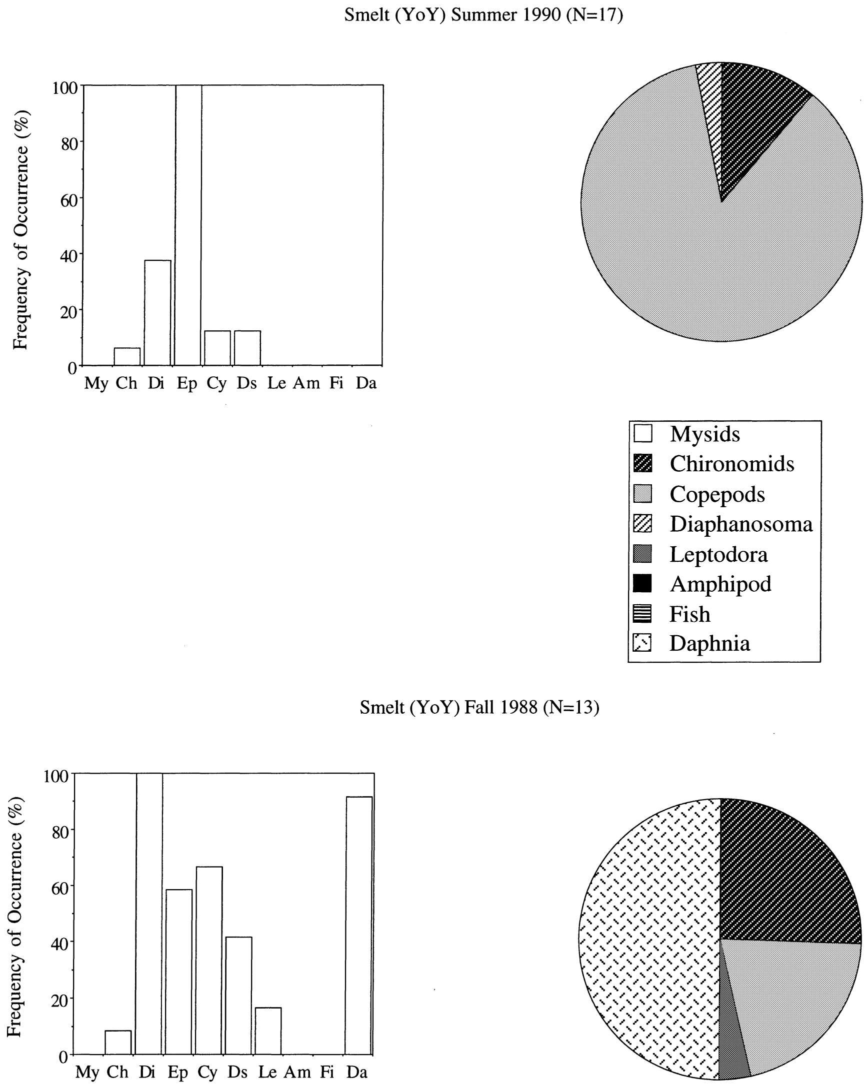

Fig. 1. Percent frequency of occurrence (bar graphs) of YoY smelt diet in Lake Washington, for summer and fall. My=*Neomysis mercedis*, Ch=Chironomid larvae, Di=*Diaptomus ashlandi*, Ep=*Epischura nevadensis*, Cy=*Cyclops bicuspidatus*, Ds=*Diaphanosoma*, Le=*Leptodora kindtii*, Am=Amphipods, Fi=Fish larvae, Da=*Daphnia* spp., and percent composition by dry weight (pie graphs) of prey types in YoY smelt diet.

mass was higher in smelt stomachs during winter than any other season. Most of the *Daphnia* observed during winter occurred in samples collected in March.

We began to find fish in smelt stomachs in spring, although <1% contained fish (Fig. 3); identifiable fish prey were sculpin (*Cottus* sp.) larvae. About 40% of smelt consumed mysids, *Diaptomus* or *Daphnia*. *Epischura* was consumed by 20% of the fish whereas <15% consumed chironomid larvae, *Cyclops*, or amphipods. Of the eight prey types identified, mysid biomass was highest (57%), followed by copepods (24%). *Daphnia* contributed about 11% of the overall prey biomass whereas amphipods and chironomids were comparatively unimportant (Fig. 3).

The two most important features of smelt diet during summer were the common occurrence of *Daphnia* species, and the predominance of mysids (62%) in the prey weight (Fig. 3). *Daphnia* spp. were

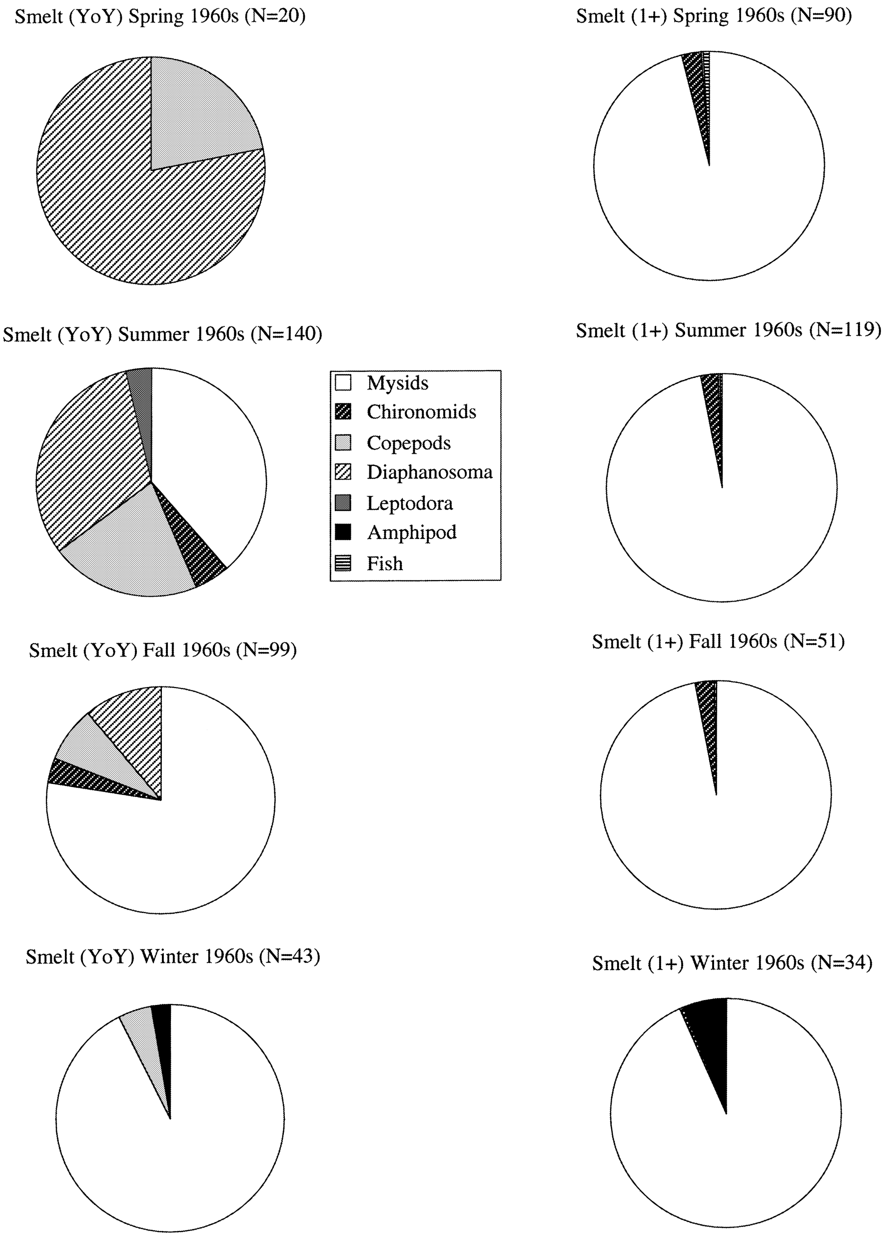

Fig. 2. Percent composition by dry weight of prey types in YoY and 1+ smelt diet. Data from Dryfoos (1965).

the second most important prey on a dry weight basis (20%). Fish and *Daphnia* prey biomass were higher during summer than in any other season. In contrast, the contribution of copepod species to smelt diet seemed negligible during the summer.

During fall, dry weight of prey was primarily mysids (50%), amphipods (29%), and *Daphnia* (16%). Fish, *Leptodora*, copepod species, and chironomid larvae were also found in stomachs but were of minor importance (Fig. 3). About 40% and 75% of fish consumed mysids and *Daphnia*, respectively. Less than 35% consumed any of the other prey species.

The number of yearling and older smelt with mysids in their gut declined from about 74–82% (spring–fall

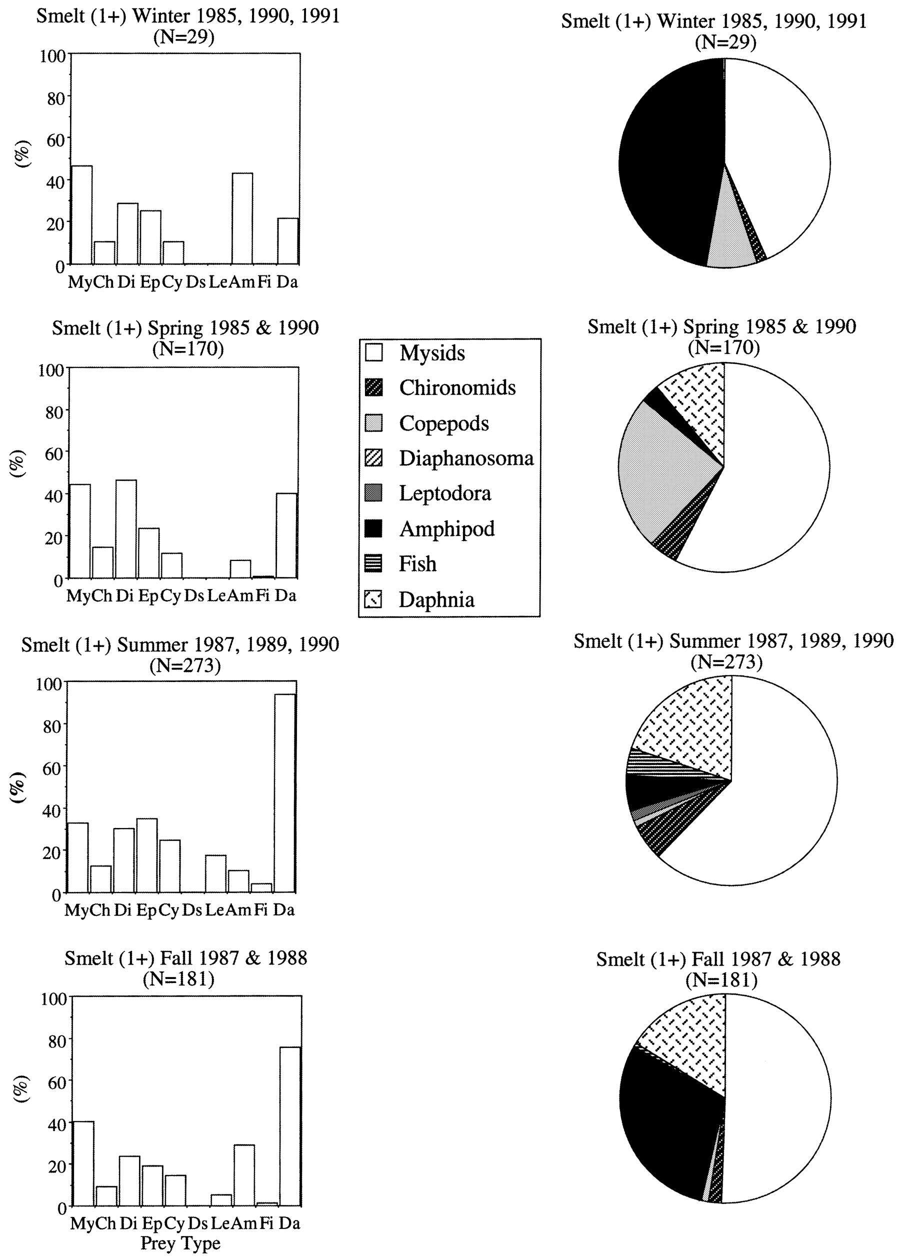

Fig. 3. Percent frequency of occurrence (bar graphs) of 1+ smelt diet in Lake Washington for winter, spring, summer and fall. My=*Neomysis mercedis*, Ch=Chironomid larvae, Di=*Diaptomus ashlandi*, Ep=*Epischura nevadensis*, Cy=*Cyclops bicuspidatus*, Ds=*Diaphanosoma*, Le=*Leptodora kindtii*, Am=Amphipods, Fi=Fish larvae, Da=*Daphnia* spp., and percent composition by dry weight (pie graphs) of prey types in 1+ smelt diet.

1960s) to about 40% (spring–fall 1980s and 1990s). *Neomysis* biomass in 1960s (Fig. 2) decreased from about 93–97% (Dryfoos, 1965) to about 50–62% in the 1980s and 1990s. Furthermore, from the 1960s to the present, there has been an apparent increase in the size at which smelt begin to feed on mysids, from 30 to about 65 mm, as well as a decrease in the number of mysids ingested (Fig. 4).

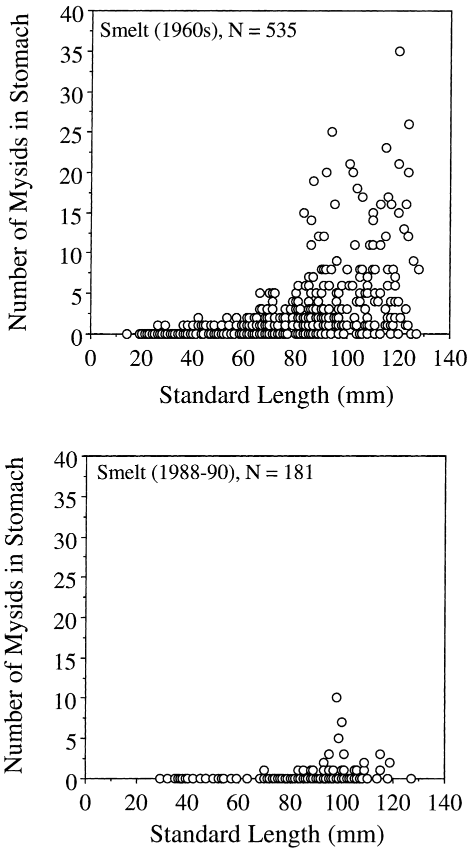

Fig. 4. Number of mysids observed in the stomachs of smelt plotted against standard length. Above are data for smelt diet in 1960s (Dryfoos, 1965). Below are data for smelt diet from 1988 to 1990. N=Number of fish with food in the stomachs.

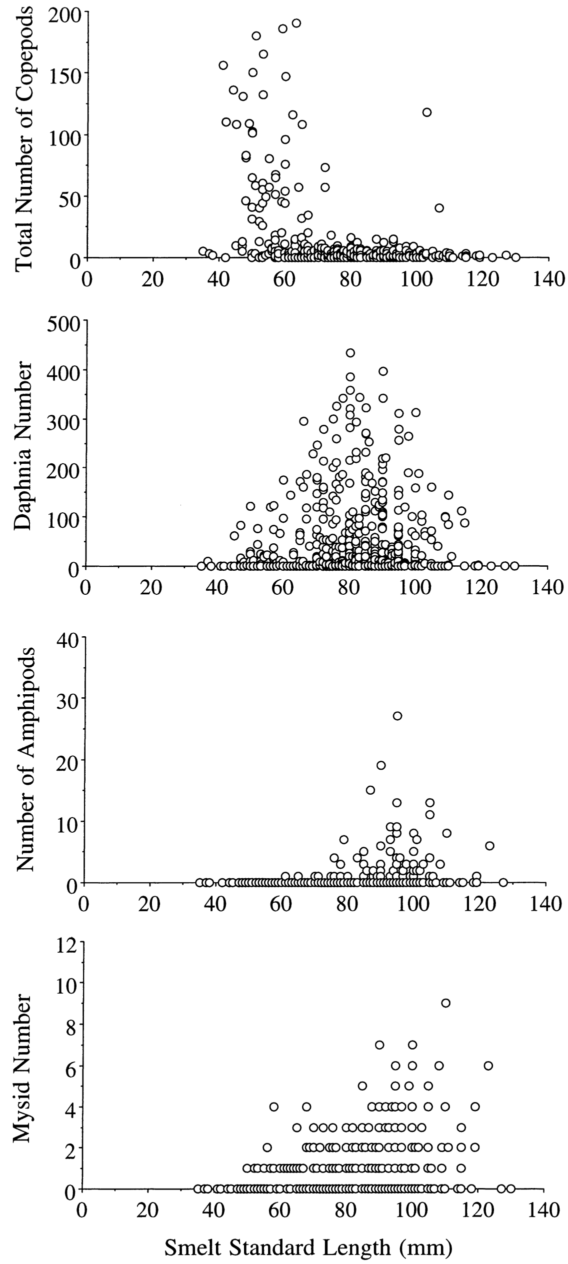

Fig. 5. Relationship between numbers of prey (copepods, *Daphnia*, amphipods or mysids) observed in smelt diet and smelt standard length.

3.3. Diet diversity, growth, and ontogenetic shift in the number and type of prey consumed by longfin smelt

In 1960s when mysids were more abundant than at present, a lower diversity (~0.07 in summer or fall) was observed for the diet of adult smelt than at present (~0.60).

We pooled all stomach content data collected from various seasons and years to examine the relationship between smelt size and type of prey consumed. The number of different types of prey consumed by smelt varied with smelt size (Fig. 5). The peak in consumption of the smallest prey (copepods) occurred at about 55, 80 mm for *Daphnia*, and the largest prey, amphipods and mysids, at about 100 mm.

Mean size at age of smelt for the 1990 YC was similar to that of 1962 YC during the first summer in Lake Washington when they were about 4–6 months

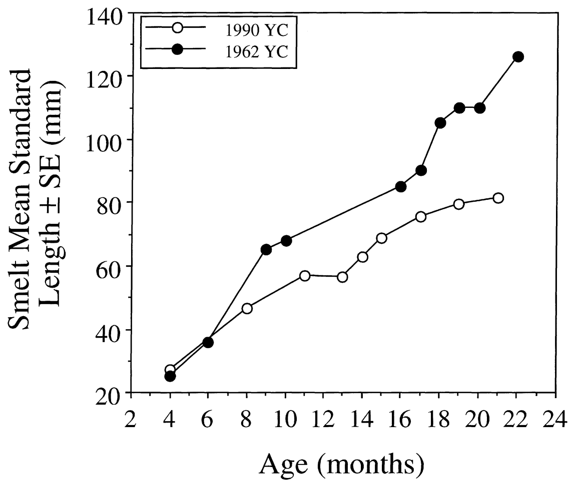

Fig. 6. A comparison of longfin smelt mean size at age (in months) for the 1962 YC and 1990 YC.

old (Fig. 6). Thereafter, mean size at age was lower for the 1990 YC fish.

3.4. *Relationship between size of mysids, amphipods and chironomid larvae consumed by smelt, and fish length*

Data collected from various seasons, 1985–1987, were combined and used to examine prey size as a function of smelt size. A significant negative correlation (Spearman's rank correlation $\{r_s\}=-0.30$, $P<0.0005$, $n=154$) between mean mysid telson length in stomachs and fish length (Fig. 7(a)) was obtained. However, mean telson length observed in smelt stomachs also varied between seasons (Fig. 7(b)). Thus, we examined the relationship between mysid size and smelt length on a seasonal basis. A simple linear regression showed no significant association in winter ($n=22$, $F=0.47$, $P=0.50$, $r=0.15$), spring ($n=38$, $F=0.67$, $P=0.417$, $r=0.136$), summer ($n=70$, $F=0.07$, $P=0.797$, $r=0.013$) or fall ($n=17$, $F=2.15$, $P=0.164$, $r=0.35$). Mysids reproduce twice a year (Murtaugh, 1983), with spring and fall cohorts. According to Murtaugh (1989), mature gravid females are larger in spring (February–July) than in fall (July–November). This difference in size may explain why the mean telson length of mysids consumed by smelt from January to June is higher than from August to November.

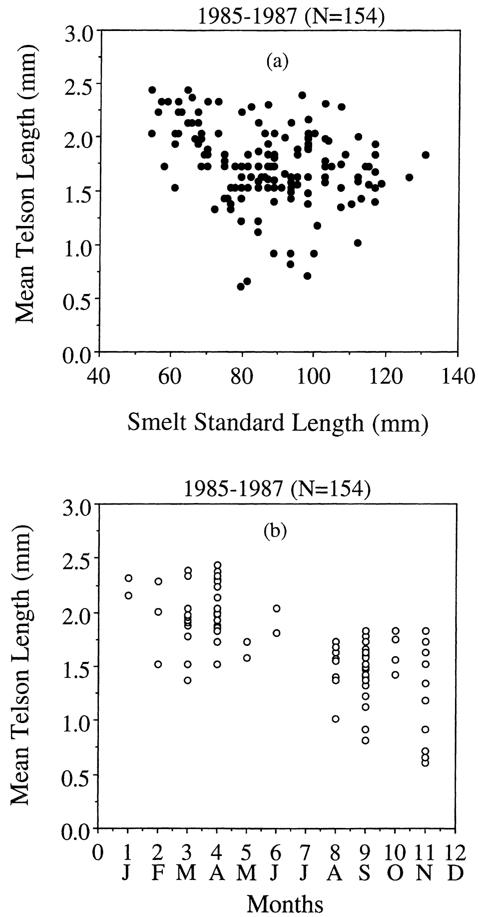

Fig. 7. (a) Relationship between mean length of mysid telsons observed in the gut of longfin smelt and smelt standard length. (b) Relationship between mean length of mysid telsons observed in the gut of longfin smelt and months. Fish collected from 1985 to 1987 were pooled.

There were also no obvious relationships between smelt size and amphipod and chironomid larvae sizes observed in smelt gut.

4. Discussion

4.1. *Smelt diet in the 1980s/1990s compared to the diet in the 1960s*

Our study shows (Figs. 1–3) that a change has occurred in smelt diet since the 1960s, both in terms of relative prey biomass and species composition.

These changes in the feeding habits of longfin smelt are related to the changes that have occurred in the Lake Washington watershed, and in the zooplankton composition in Lake Washington following its recovery from eutrophication (Edmondson and Litt, 1982; Edmondson and Abella, 1988).

It is believed (Edmondson and Abella, 1988) that revetments of the banks of the Ceder river, where smelt spawn, allowed for better egg survival, and hence an increase in smelt recruitment beginning in the late 1960s. As a consequence, the abundance of *Neomysis* (a preferred prey of smelt) declined drastically. Because *Neomysis* are efficient predators on *Daphnia* (Murtaugh, 1981b; Chigbu and Sibley, 1994c), a decrease in mysid density was one of the major factors that resulted in increased abundance of *Daphnia* in the lake starting in 1976 (Edmondson and Litt, 1982; Edmondson and Abella, 1988).

Unlike in the 1960s when *Daphnia* were absent or scarce in Lake Washington, *Daphnia* species, which are now among the dominant crustacean zooplankton in the lake in summer (Edmondson and Litt, 1982; P. Chigbu, unpublished data), constitute an important prey of both YoY and 1+ smelt. *Diaphanosoma* were common in the diet of YoY smelt in 1960s. We still observed them in YoY smelt during this study, but generally they were comparatively less abundant in summer and fall than during Dryfoos' study (Dryfoos, 1965). This corresponds with their low occurrence in the lake relative to the 1960s level (Edmondson and Litt, 1982).

Amphipods were never reported to comprise more than 6.5% of prey biomass in the 1960s but currently are among the dominant prey of 1+ smelt in winter and fall. This may reflect a higher abundance of amphipods in the lake at present compared to the 1960s when the lake was eutrophic.

An increase in the diversity of smelt diet at present when compared to the diet in the 1960s is consistent with niche theory which stipulates that when a "preferred" prey is abundant, breadth of diet is more limited than during seasons when such prey are scare (Wootton, 1990). Smelt, therefore, seem to feed on other prey during seasons when mysids are scarce.

We observed that smelt prey more on zooplankton, particularly *Daphnia*, as well as on amphipods and chironomids following the reduction in mysid abundance. It might be argued that smelt are currently feeding on *Daphnia* spp. because *Daphnia* are much more abundant in the lake (Edmondson and Litt, 1982) than in the 1960s. However, density of *Neomysis* in the Lake (Murtaugh, 1981a; Chigbu, 1993) and reduced number of mysids in smelt gut (Fig. 4) suggest that mysids are scarce in the lake relative to 1960s level. Thus yearling and older smelt appear to be feeding on *Daphnia* to compensate for the loss of mysids, and thus optimize energy intake.

4.2. Diet composition in relation to smelt size

The observed change in prey type with smelt size indicates increasing preference for larger prey such as mysids and amphipods as smelt grow. During spring and early summer when smelt first enter the lake, their diet is composed of copepod species, even though *Daphnia* are abundant in the lake. From first fall, smelt begin to feed on *Daphnia*, and subsequently consume larger prey such as mysids, amphipods, and chironomids. This shift in diet composition with smelt growth may also be partly due to seasonal variation in prey availability and smelt distribution. However, diet of 1+ smelt collected in July 1989 (Sibley and Chigbu, 1994) also suggest that larger smelt (>80 mm) preferred larger prey such as mysids, amphipods, and fish whereas smaller smelt (<80 mm) preferred smaller prey such as *Daphnia* and copepod species; ontogenetic shifts in diet to optimize energy acquired per time spent foraging are common features of fish (Werner and Gilliam, 1984).

Although piscivory may be important in some smelt species, piscivory by longfin smelt in Lake Washington appears insignificant compared with studies conducted in the Great Lakes (Stedman and Argyle, 1985; Brandt and Madon, 1986; Loftus and Hulsman, 1986). The few fish observed in smelt stomachs were sculpin (*Cottus* sp.) larvae.

Young smelt were not captured in the 3 m IKMT samples prior to July of each year in which the fish were recruited into the limnetic zone during this study. Hence, we have no information on their feeding habits when they first enter Lake Washington from the Cedar River. Dryfoos (1965) who took post-larval smelt in spring using a 2 m IKMT found mainly *Diaptomus* and *Diaphanosoma* in stomachs during their first spring in the lake. Naesje et al. (1987) found pennate diatoms in the diet of smelt (*O. eperlanus*) in a Norwegian lake during first feeding; rotifers and copepod nauplii and copepodids occurred rarely. As they grew, cladocerans and copepods became important in their diet. To the contrary, Strelnikova and Ivanova (1982) found that the larvae of *O. eperlanus* ate only rotifers and small copepods in Rybinsk reservoir (USSR) when they began external feeding.

4.3. Comparison of smelt growth in 1980s/1990s and 1960s

Associated with changes in smelt diet is a decrease in smelt body size. There was about 25% reduction in weight at maturity of even year classes of smelt, 1960–1990s (Chigbu and Sibley, 1994a), whereas at least a 50% reduction in the number of mysids consumed by smelt has occurred (Chigbu and Sibley, 1994b; see Fig. 4). In the 1960s, smelt preyed on mysids in their first summer and fall; we found no mysids in smelt stomachs in their first summer and fall. Finding prey of optimal size is important for fish growth, failure of which results in stunting (Mills et al., 1989). Sokolova (1991) observed improvements in fish growth in bodies of water where there was increased mysid abundance. A higher abundance of smelt in the 1990s than the 1960s, with accompanying intraspecific competition for the scarce mysids, may explain why the difference in growth between the 1962 and 1990 year classes became obvious from the first fall (Fig. 6).

This study supports Moulton's hypothesis that the reduction in smelt growth from 1962 to 1966 year classes was due to an increase in smelt abundance and a consequent decline of mysid abundance (Moulton, 1974). Moreover, the size at age of the 1990 year class smelt was smaller than the 1966 and 1968 year classes (Moulton, 1974; Chigbu and Sibley, 1994a), perhaps due to a further increase in smelt abundance in the lake.

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