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Abundance and distribution of *Neomysis mercedis* and a major predator, longfin smelt (*Spirinchus thaleichthys*) in Lake Washington

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Abstract

Seasonal variations in the horizontal and depth distributions of *Neomysis mercedis* and longfin smelt (*Spirinchus thaleichthys*) were examined using night-time mid-water trawl and Bongo net samples collected in Lake Washington from July 1989 to February 1992. Mysid density varied spatially, seasonally and yearly. For example, during summer, and fall (odd years), mysid abundance was highest in the northern, and lowest in the southern sections of the lake, except in December 1991 when they were uniformly distributed. In fall (November 1990), mysid density was highest in the central basin of the lake. Furthermore, in winter of even years, highest mysid density occurred in the southern region of the lake, but in the central region in winter (February) of odd year. Longfin smelt horizontal distribution also varied seasonally. For example, density of the 1988 YC smelt (1+) was highest in the northern area of Lake Washington in summer but highest in the southern area in fall. During winter, distribution seemed random. The abundance of the 1990 YC smelt (YoY) was also highest in the northern section of the lake in summer, but highest in the southern section in fall; density remained high in the southern section in winter. But, by late spring when they were more than one year old, the distribution had changed such that highest abundance occurred in the northern and mid-section of the lake. By winter when they were about two years old and about to begin spawning, density had become highest again in the southern section. These suggest extensive movement of mysids and smelt from one area to another, perhaps driven by wind-induced water currents in the lake.

Depth distribution patterns of mysids and smelt are discussed. Smelt were captured mainly in the shallow strata (8 m) of the lake during all seasons except during winter when they predominated at 50 m. Mysids were also mainly caught in the shallow strata of the lake during all seasons, although a significant proportion occurred at greater depths (> 30 m).

The abundance of both species was positively correlated in spring and summer but negatively correlated in fall. A poor correlation was observed in winter. Negative correlation in fall was primarily due to the occurrence of mysids and smelt in different areas of the lake whereas poor correlation in winter was particularly due to their occurrence at different depths. Because of considerable overlap in the distribution of both species in the lake, mysids face a high risk of predation by smelt. This piece of information is consistent with the hypothesis that smelt control mysid abundance in Lake Washington.

Introduction

Fish predation is a major factor affecting the abundance of cladoceran zooplankton (Brooks & Dodson, 1965; Post & Mcqueen, 1987) and mysids (Siegfried, 1987; McDonald et al., 1990; Kjellberg et al., 1991; Chigbu & Sibley, 1998) in lentic freshwater ecosystems. Heavy predation on prey populations may depress prey biomass, reduce the size of individual organisms and alter prey distributions. For predators to control their prey, there must be a considerable degree of spatial overlap between them (Williamson et al., 1989; Roche, 1990) as well as high prey vulnerability. To assess the impact of a predator on their prey and to understand the underlying control mechanism, knowledge of the population size, together with spatial and temporal distribution of the two species, is a pre-requisite (Williamson & Stoeckel, 1990).

Neomysis mercedis Holmes in Lake Washington selectively feed on cladocerans (Murtaugh, 1981a, b, c), and can compete with planktivorous fish for food. Despite the fact that the night-time vertical distribution of mysids, especially *Mysis* spp., has been well studied (Beeton, 1960; Hakala, 1978; Bowers, 1988; Rudstam et al., 1989; Lehman et al., 1990), few studies have examined the spatial and temporal association of mysids and their predators (Janssen & Brandt, 1980; Levy, 1991).

Dryfoos (1965) observed a positive association between the abundance of longfin smelt (*S. thaleichthys*) and mysids in Lake Washington, although a detailed analysis was not presented. Moreover, the nocturnal mean depth distribution of *Neomysis* appeared to increase between 1962 and 1976 (Eggers et al., 1978) and might have affected the extent of spatial overlap between smelt and mysids. Recently, we examined aspects of smelt (*S. thaleichthys*) interactions with their zooplankton prey, especially mysids (Chigbu & Sibley, 1994a, b; 1998). The objective of this present study was to assess seasonal variations in the horizontal and depth distributions of mysids and longfin smelt (*S. thaleichthys*).

Materials and methods

Mysid and longfin smelt collection

Midwater trawl surveys were conducted from July 1989 to February 1992 in the pelagic zone of Lake Washington using a 3 m Isaacs-Kidd midwater trawl (IKMT), the primary gear used previously to estimate pelagic fish and mysid abundance in the lake (Dryfoos, 1965; Traynor, 1973; Eggers et al., 1978). The codend of the trawl is made of a 5 mm knotless nylon whereas the upper portion is made of 3.2 cm stretch mesh (Chigbu, 1993).

The upper part of the net has essentially zero mysid retention efficiency because of the large mesh size (3.2 cm) in that portion. As *Neomysis* is roughly 3 mm in length at the time of release from the brood pouch (P. Chigbu, personal observation), attains a maximum size of about 18 mm and varies seasonally in size, the 5 mm knotless nylon at the codend would, at least, undersample mysids less than or equal to 5 mm in length. Therefore, the population estimates made using IKMT catch are indexes of mysid abundance rather than reliable measures of absolute population size. During each period, sampling was conducted on two consecutive nights in five areas of the lake (Figure 1), and at various depths (8–50 m). On the first night, areas 5 to 3 were sampled whereas areas 1 and 2 were sampled on the second night. Sampling order and specific depths sampled were 8, 15, 22, 30, 36 and 50 m except where lake depth precluded trawling at 36 or 50 m. A maximum of 25 and a minimum of 9 depth strata were sampled. In areas 1 and 5 four depth strata in the range of 8 to 30 m were sampled. Six strata were sampled in areas 2 and 3 (8–50 m) and five strata (8–36 m) were sampled in area 4. Thus areas 1 and 5 are the shallowest, whereas 2 and 3 are the deepest sections of the lake.

Trawling usually began just after sunset, a time when both mysids and smelt are readily caught in the water column (Eggers et al., 1978). Trawling duration and speed were maintained at 10 min and about 5 knots, respectively. After each trawl, the net was rinsed in a plastic tub. All smelt and mysids caught were preserved in 10% formalin and subsequently counted. Generally all smelt caught, and from 36 to 640 randomly selected mysids were measured for each sampling date. Mysid measurements were from the tip of the rostrum to the base of the telson. Because IKMT undersampled small mysids, mysid sizes reported here are biased especially during spring and summer when juveniles are released into the lake. During counting, the fish were separated into two year classes; subyearling and 1+ smelt, guided by the fact that length frequency distributions showed two distinct year classes with little or no overlap (Chigbu & Sibley, 1994b). The 1+ smelt are the major predators on mysids (Dryfoos, 1965; Chigbu & Sibley, 1994a). During eight field trips, from November 1990 to February 1992, mysids were sampled at five stations mentioned above, using IKMT and a Bongo net, to compare mysid sizes, and distribution patterns for the two sampling gear. The Bongo net was towed vertically from maximum depths of 30 to 55 m to the surface depending on the maximum depth of the lake at the site sampled. One to three tows were made in each area. The Bongo net used was made of 500 and 333 micron mesh. Night-time vertical or oblique tows are effective for sampling mysid populations (Grossnickle & Morgan, 1979), and have been used by many mysid population ecologists (Morgan, 1980; Janssen

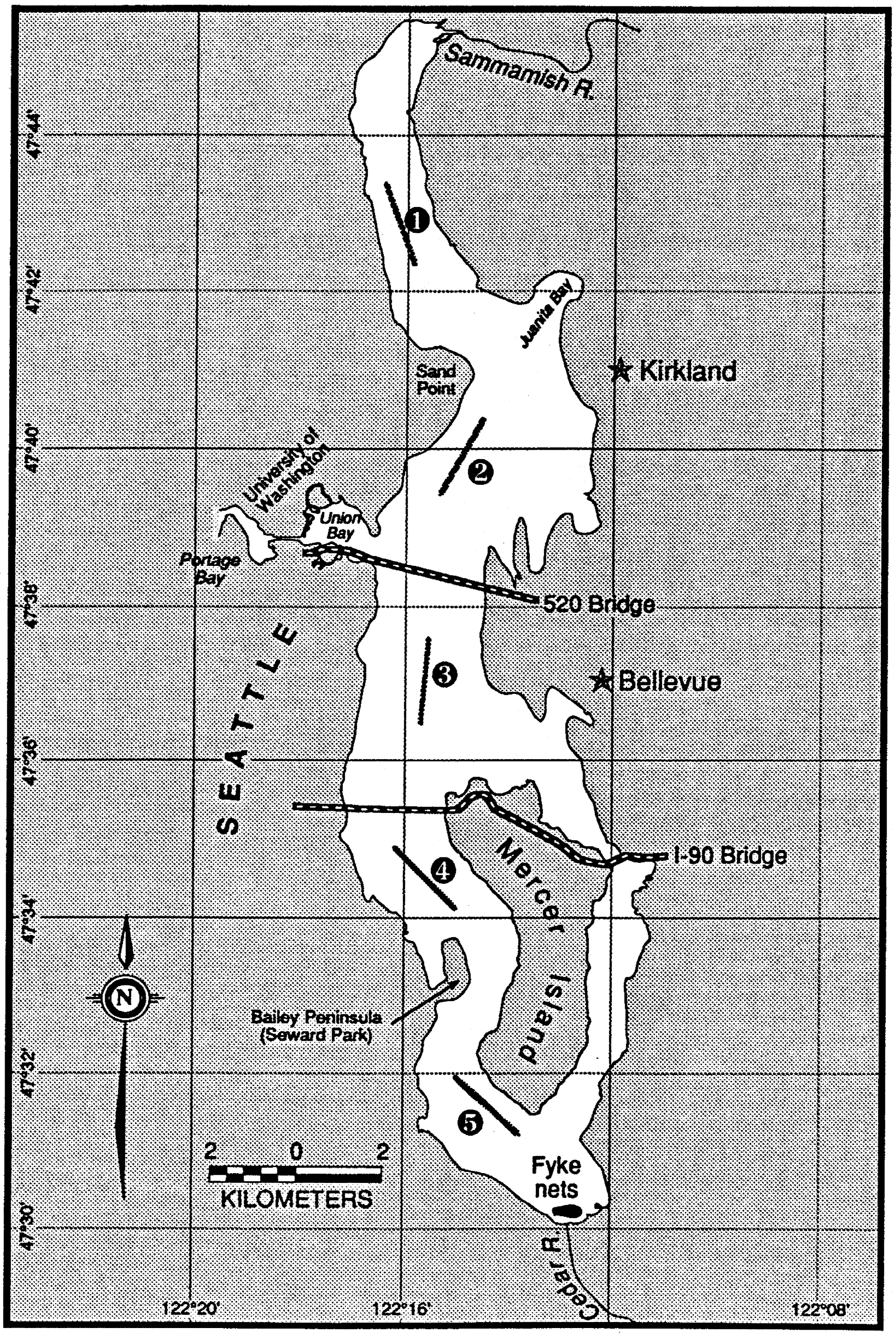

Figure 1. Map of Lake Washington showing the sampling stations.

& Brandt, 1980; Nero & Davis, 1982; Rudstam et al., 1986).

Estimation of mysid and smelt abundance, and assessment of their distribution

To estimate fish or mysid abundance, the lake was stratified by depth and area, and the volume of water in the limnetic zone of each stratum was estimated using morphometric data (Anderson, 1954). The effective mouth opening of the trawl during towing was assumed to be about 6.0 m^2 (Traynor, 1973). The volume (V) of water sampled by the net during a 10 min tow was therefore estimated using the formula:

$$V = \chi(d),$$

where χ = cross sectional area of the IKMT and d = distance covered during a 10 min tow at 5 knots.

For mysids, volume of water sampled by the trawl was estimated using the area of a 0.62 m ring at the cod-end of the trawl to which a net with a 5 mm stretch mesh was attached, and the distance covered during the trawl.

Fish or mysid abundance (Y) was calculated for each stratum with the formula:

$$Y = v^* z,$$

where v = volume of water in each stratum and z = density of fish in the stratum (numbers per cubic meter).

Population density for each area was calculated by summing population estimates for all depth strata in that area and dividing by the total volume of water in the area. For samples collected with Bongo nets, mysid abundance was also expressed as numbers per cubic meter.

The degree of association between mysids and smelt was determined by Spearman's rank (r_s) correlation analysis using catch per trawl data. We assessed seasonal variations in night-time depth distributions of mysids and smelt using trawl samples collected from area 3 (a deep, central station), although comparable data exist for other areas. For each season, we calculated mean number of mysids or smelt captured per trawl at each depth. Seasons are herein defined as summer = July to September; fall = October to December; winter = January to March; and spring = April to June (Dryfoos, 1965).

Spatial patterns in mysid consumption by smelt

Gut contents of fish samples collected from various areas in spring 1985 and fall 1987 were examined and the number of mysids observed was used to determine if spatial differences in the number of mysids consumed reflect seasonal differences in mysid distribution observed in spring and fall in this study.

Results

Abundance, size and night-time horizontal distributions of mysids and smelt

Presented in Figures 2–4 are the abundance and horizontal distributions of mysids and smelt (1988 to 1990 year classes). The even year classes of smelt (Figures 2 and 4) were clearly more abundant than the odd year class (see Figure 3). For example, 1+ smelt mean CPUE in December 1989 (19.88 $\pm$ 5.62 SE) and 1991 (38.84 $\pm$ 6.55 SE), and in November 1990 (3.04 $\pm$ 0.51 SE) were significantly different (ANOVA, F-test = 61.08, P = 0.0001, df = 2, 72). A multiple comparison using Scheffe F-test indicated that CPUE were significantly higher in December 1989 and 1991 than in November 1990 ($P < 0.05$). This presented us with the opportunity to examine mysid abundance and distribution during two years (1989 and 1991) of high 1+ smelt and one year (1990) of low 1+ smelt abundance. Mysid abundance was generally higher during even years than during odd years (Figures 2–4). For example, mysid CPUE was higher in July (69.4 $\pm$ 20.1S.E Vs 10.2 $\pm$ 4.1S.E; $P < 0.01$) and November (273.2 $\pm$ 41.2S.E Vs 173.2 $\pm$ 37.7S.E; $P < 0.05$) of even years than odd years (Mann-Whitney U-test).

(a) 1 + smelt (1988 YC) and mysid (July 1989 to January 1990 sampling period) size, abundance and distribution

During summer (July 1989) and fall (December 1989), 1+ smelt and mysid abundance varied among lake areas (Figure 2a, b; d, e). In winter (January 1990), 1+ smelt abundance showed no definite trend with lake area whereas mysid abundance varied with area (Figure 2c, f). As 1+ smelt size increased from 79.1 $\pm$ 0.3 mm (mean $\pm$ SE) in July 1989 to 85.8 $\pm$ 0.4 mm in December 1989, their distribution shifted from one with highest abundance in area 1 (Figure 2a) to highest abundance in area 5 (Figure 2b). By January 1990, 1+

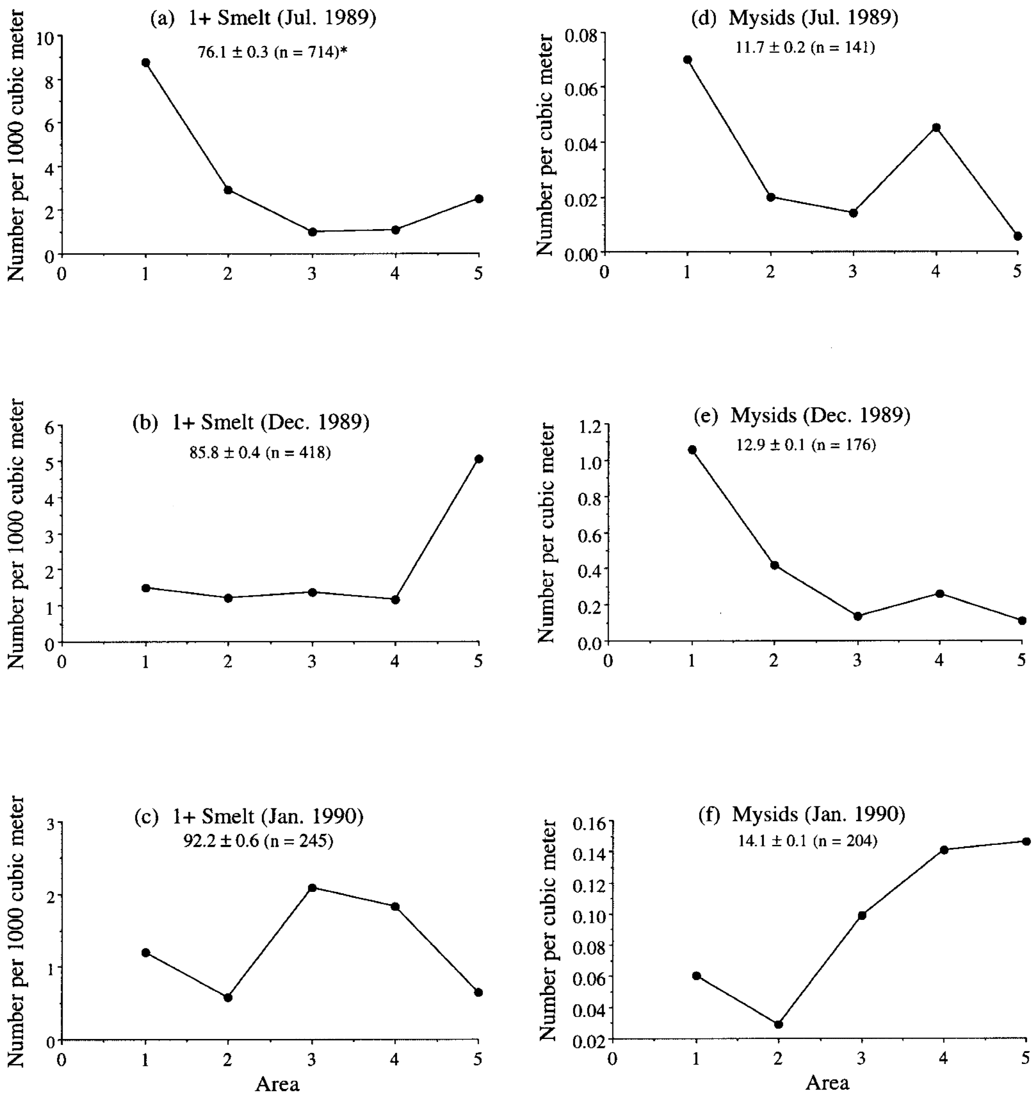

Figure 2. The horizontal distribution of 1+ smelt (1988 YC) and mysids *Neomysis mercedis* in Lake Washington, based on samples collected with IKMT. *Smelt/mysid mean size ± standard error (mm).

smelt were about 92.2 ± 0.6 mm in size, comparatively low in abundance, and showed no trend with area (Figure 2c).

From July 1989 to January 1990, mysid size increased from 11.7 ± 0.2 mm to 14.1 ± 0.1 mm and the pattern of distribution also changed from their predominance in area 1 to area 5 (Figure 2d–f).

(b) 1 + smelt (1989 YC) and mysid (April 1990 to February 1991 sampling period) size, abundance and distribution

The distribution of YoY smelt (1989 YC) is not presented here because very few of such fish were caught. From April 1990 to February 1991, 1+ smelt densities were much lower than during the period of July 1989 to January 1990, as the highest density in an area during each trip never exceeded 2 fish 1000 m^{-3}(Figure 3 a–d). It was only in July 1990 that a definite trend in 1+ smelt abundance was observed; the occurrence of the highest density (2 fish 1000 m^{-3})

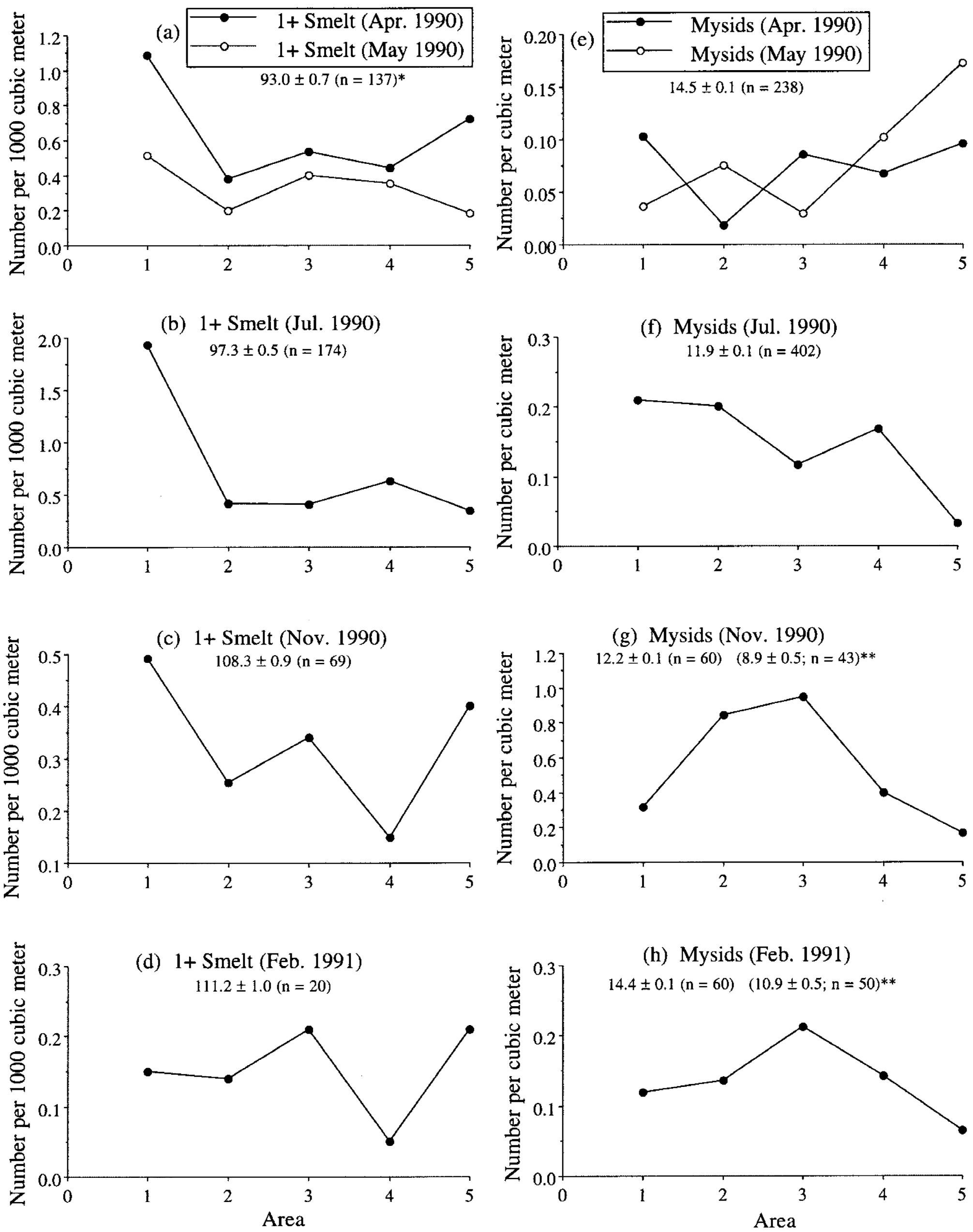

Figure 3. The horizontal distribution of 1+ smelt (1989 YC) and mysids *Neomysis mercedis* in Lake Washington, based on samples collected with IKMT. *Smelt/mysid mean size ± standard error (mm). **Mysid mean size ± standard error (mm) based on samples collected with Bongo net.

in area 1 (Figure 3b) is consistent with the observation in July 1989 (Figure 2a).

Virtually all mysid data during this period suggest that distribution varied seasonally. During spring, no definite trend in mysid distribution was observed in April 1990, but mysid density was highest in area 5 ($0.17\ m^{-3}$) during May 1990 (Figure 3e). The presence of a higher mysid density in area 1 ($0.21\ m^{-3}$) than in area 5 ($0.03\ m^{-3}$) in summer (July 1990; Figure 3f) is in agreement with mysid distribution in July 1989. When the distributions in November 1990 (fall) and February 1991 (winter) were compared with those

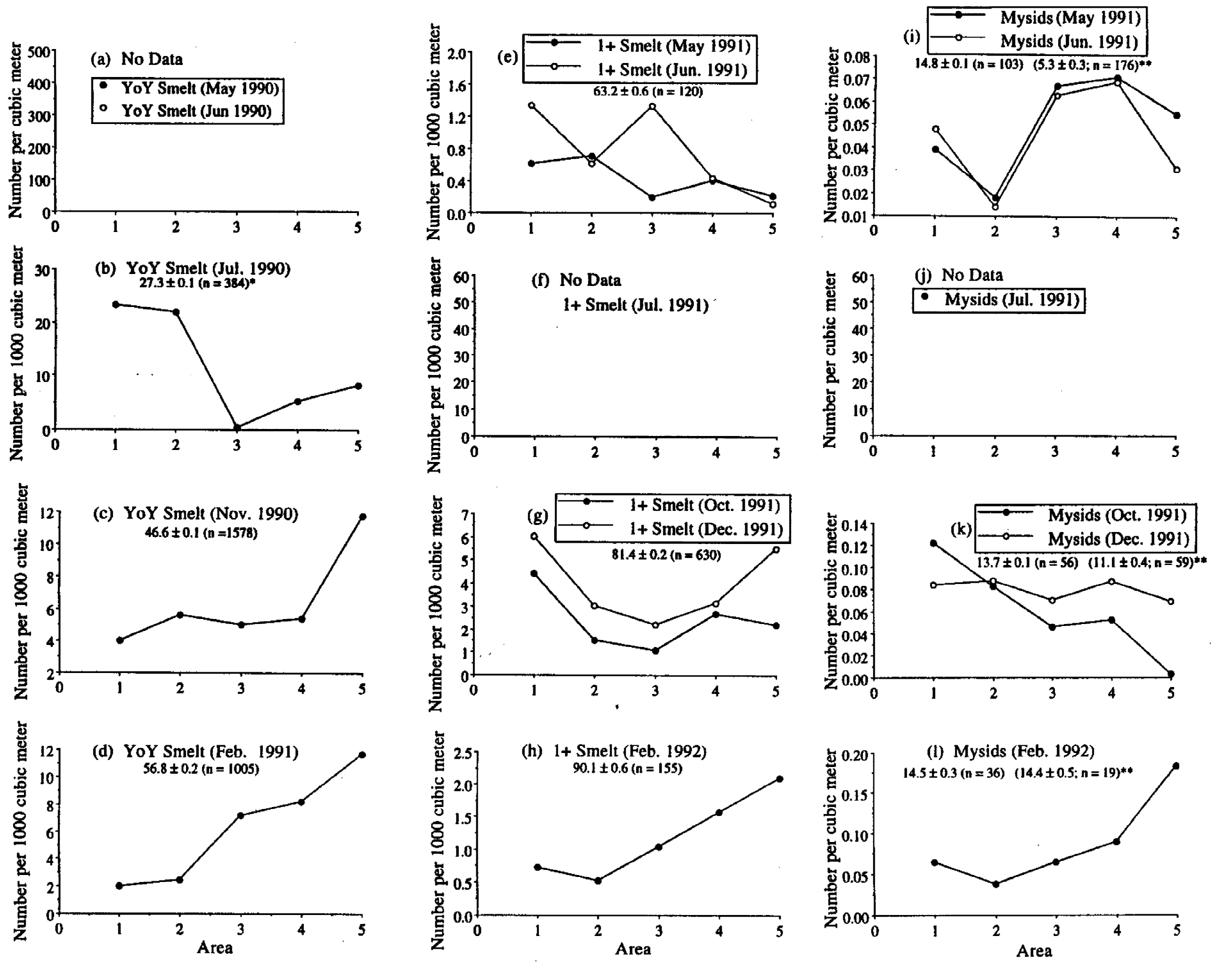

Figure 4. The horizontal distribution of 1+ smelt (1990 YC) and mysids *Neomysis mercedis* in Lake Washington, based on samples collected with IKMT. *Smelt/mysid mean size ± standard error (mm). **Mysid mean size ± standard error (mm) based on samples collected with Bongo net.

of December 1989 and January 1990 respectively, an important difference was noted (see Figure 3g, and h). The highest densities (0.84 and 0.95 m^{-3}) were observed in the central region of the lake (areas 2 and 3) in November 1990, and February 1991 (0.21 m^{-3}, area 3) as opposed to the shallow areas in December 1989 (area 1) and January 1990 (areas 4 and 5).

(c) Smelt (1990YC) and mysid (July 1990 to February 1992 sampling period) size, abundance and distribution

No YoY smelt were captured in spring 1990 (Figure 4a). The horizontal distribution patterns of 1990 YC smelt beginning from their first summer to their last winter in the lake are presented in Figures 4 b–h. YoY smelt size increased from 27.3 ± 0.1 mm in July 1990 to 56.8 ± 0.2 mm in February 1991, and their density varied seasonally and spatially. They were caught mainly in areas 1 and 2 in summer (July 1990), but in area 5 in fall (November 1990) and winter (February 1991).

By spring (June 1991) when smelt size had reached 63.2 ± 0.6 mm, density had become highest in areas 1 and 3 (Figure 4e). No samples were collected in July 1991. In October 1991, 1+ smelt abundance was highest in area 1 whereas in December 1991 abundance was highest in areas 1 and 5 (Figure 4g). By February 1992, 1+ smelt had become most numerous in area 5 (Figure 4h).

From May 1991 to February 1992 (Figure 4 i–l), mysid density varied among lake area, except during December 1991 (Figure 4k). In spring (May and June

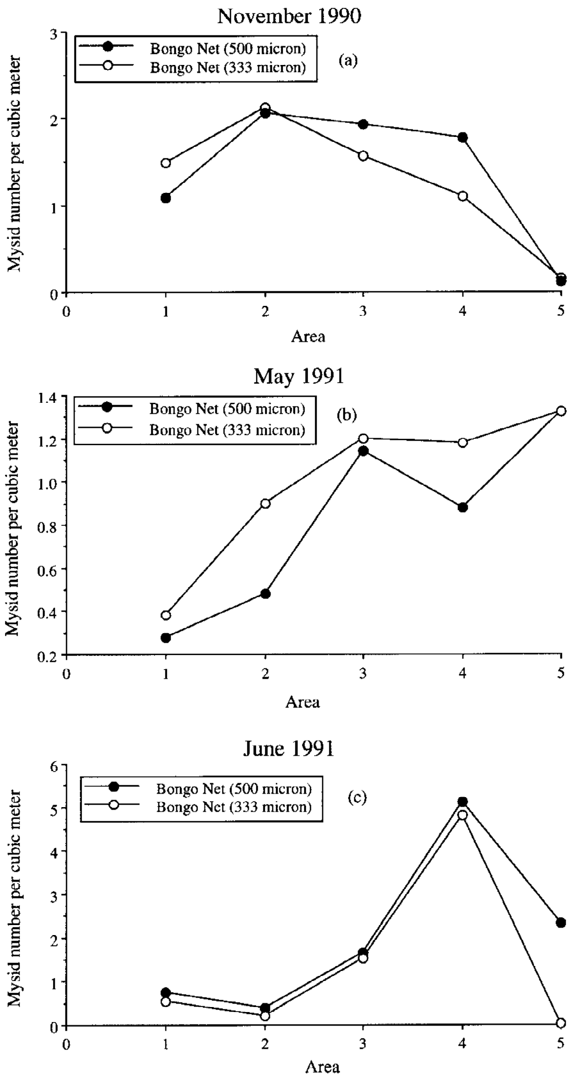

Figure 5. The horizontal distribution of mysids *Neomysis mercedis* in Lake Washington, based on samples collected with Bongo net. *Mysid mean size ± standard error (mm).

1991) when mysids were about 14.8 ± 0.1 mm in size, density was lowest in area 2 (0.01–0.02 m^{-3}) and highest in areas 3 and 4 (0.06–0.07 m^{-3}). Mysid distribution patterns in fall (October 1991) and winter (February 1992) were comparable to those observed in December 1989 and January 1990 (Figure 2e, f), respectively. Abundance generally decreased from area 1 to 5 in October 1991, but decreased from area 1 to 2 before increasing to the highest level (0.18 m^{-3}) in area 5, in February 1992 (Figure 4k & l). No samples were collected in July 1991 (Figure 4j).

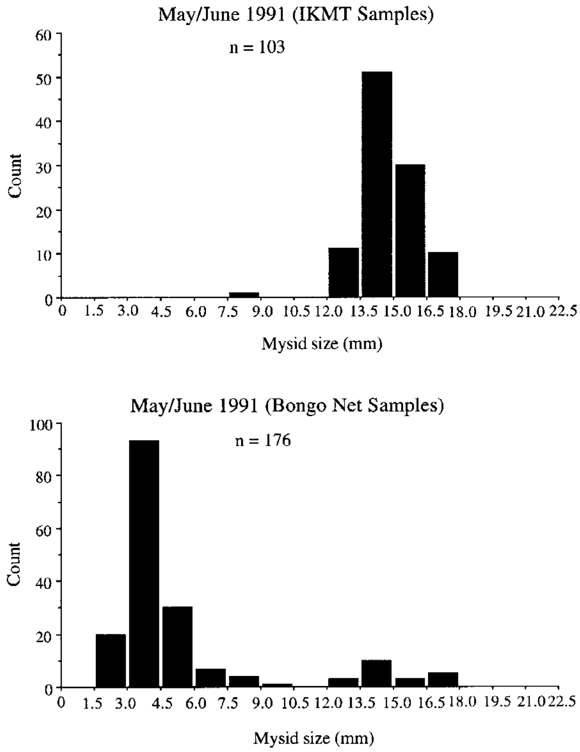

Figure 6. Size distribution of mysids *Neomysis mercedis* captured in IKMT (above) compared with size distribution of mysids captured in Bongo nets (below).

Night-time horizontal distributions of mysids: A comparison of Bongo net and IKMT samples

The horizontal distribution of mysids based on Bongo net samples was similar to the distribution based on IKMT samples Spearman's rank (r_s) corrected for ties = 0.75, $P < 0.001$, $n = 22$. For example, Figure 5a shows that Bongo net data are similar to IKMT data (Figure 3g) with respect to the areas with lowest mysid density. However, inclusion of samples collected in spring (May and June 1991), when juvenile mysids were released in the lake, resulted in a difference in distribution pattern (r_s corrected for ties = 0.27, $P < 0.20$, $n = 32$), as mysid density based on bongo net samples, generally increased from area 1 to area 3 or 4, and then levelled off (May 1991, Figure 5b), or declined (June 1991, Figure 5c). In contrast, for samples collected with IKMT, mysid density declined from area 1 to area 2, then increased to a maximum (area 3 and 4) before declining again (see Figure 4i). The differences that exist in mysid distribution patterns from IKMT and Bongo net samples collected in

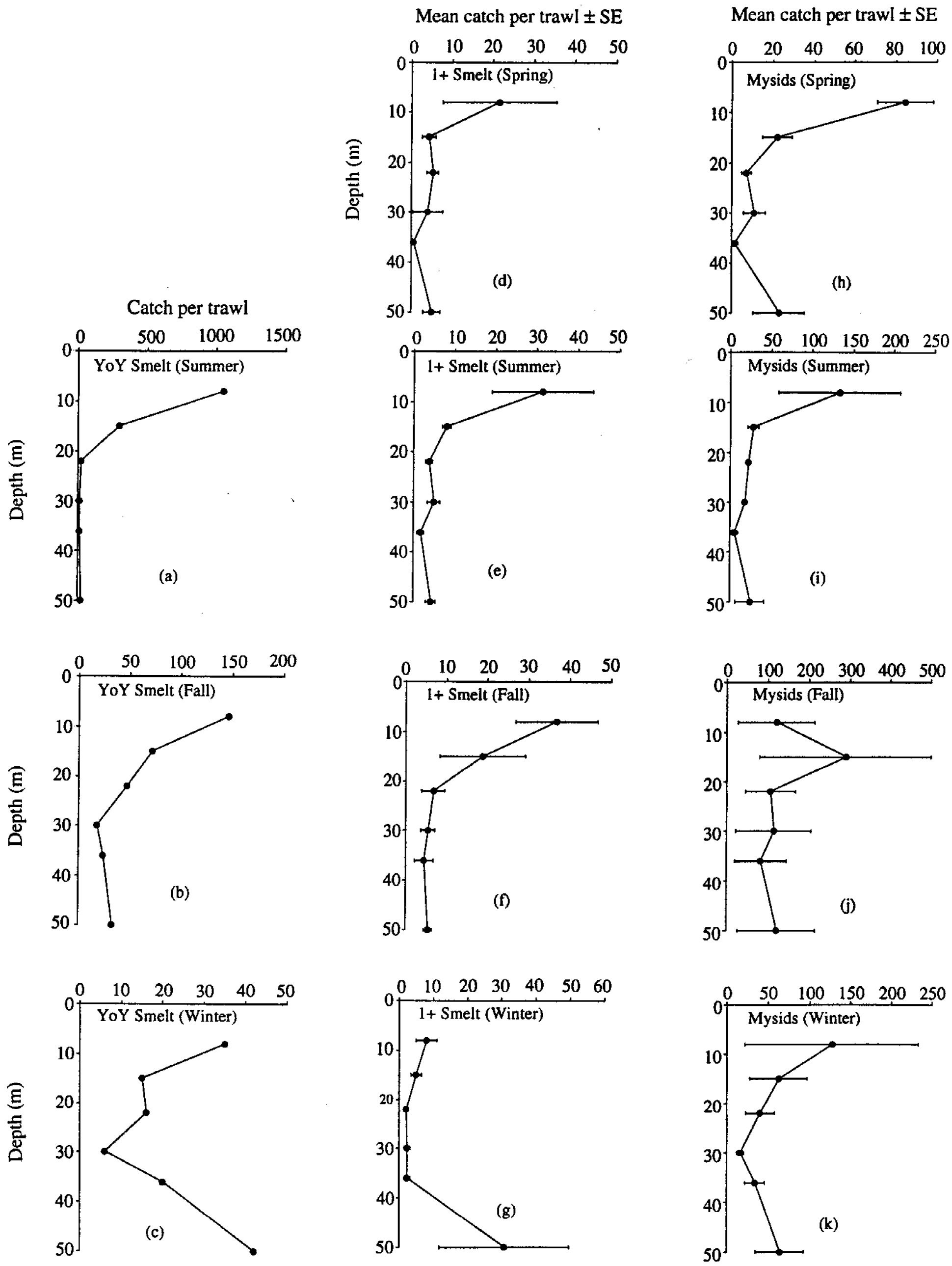

Figure 7. Night-time depth distributions of smelt and *Neomysis mercedis* in the central basin (Area 3) of Lake Washington.

spring stemmed, in part, from the fact that the IKMT failed to catch mysids < 10 mm in length (Figure 6).

Night-time depth distributions of mysids and smelt

We captured smelt mainly in the shallow water strata (8 m) from spring to fall (Figure 7). During winter, a large proportion of smelt was caught close to the lake bottom at 50 m (Figure 7c, g). Mysids also occupied shallow strata, especially during spring and summer (Figure 7h–k), even though a significant proportion remained in the deep strata (> 36 m).

Table 1. Correlations between longfin smelt and mysid abundance

Season	Year(s)	r_S^*	*n*	*P*-value
1+ smelt and mysids				
Spring (Apr.–Jun)	1990 & 1991	0.29	95	<0.005
Summer (Jul.)	1989 & 1990	0.36	42	<0.02
Fall (Nov. & Dec.)	1989 & 1991	−0.53	75	<0.0001
Winter (Jan. & Feb.)	1990 & 1992	0.01	73	0.91
Even year (all data)	1990	0.11	149	0.165
Odd year (all data)	1989 & 1991	0.23	171	<0.002
All seasons	1989–1991	0.15	320	<0.002
YoY smelt and mysids				
Summer (Jul.)	1990	0.53	25	<0.01
Fall (Nov.)	1990	−0.15	25	>0.05
Winter (Feb.)	1991	0.34	24	>0.05
All data	190 & 1991	0.44	74	<0.001

*Spearman's rank correlation.

Relationships between smelt and mysid abundance

We assessed the overall spatial association of mysids relative to smelt first by pooling all data collected during each season irrespective of the year during which they were collected. Then, all data collected during even and odd years were examined separately. Finally, all data were pooled.

Significant positive correlations between mysid and 1+ smelt abundance were observed in spring and summer, but negative correlation in fall (Table 1). During winter, correlation between the two species was poor (r_S = 0.01, P = 0.910). When all data collected during even, and odd years, and when data for all years were combined, we also noted positive correlations, although this was not significant for the even year's data (Table 1).

Mysid and YoY smelt abundance was significantly correlated during the summer (r_S = 0.53, P < 0.01), but not during fall or winter (Table 1).

Spatial variations in the number of mysids consumption by smelt, and its relationship to mysid distribution

Mean number of mysids observed in smelt gut in April 1987 and November 1987 varied among lake areas (Figure 8a, b). The differences among areas were highly significant more so in April (Kruskal-Wallis test, df = 4, H corrected for ties = 19.97, P < 0.001) than in November (Kruskal-Wallis test, df = 4, H corrected for ties = 9.59, P < 0.05). In April, lowest numbers of mysids were consumed in area 1. This was

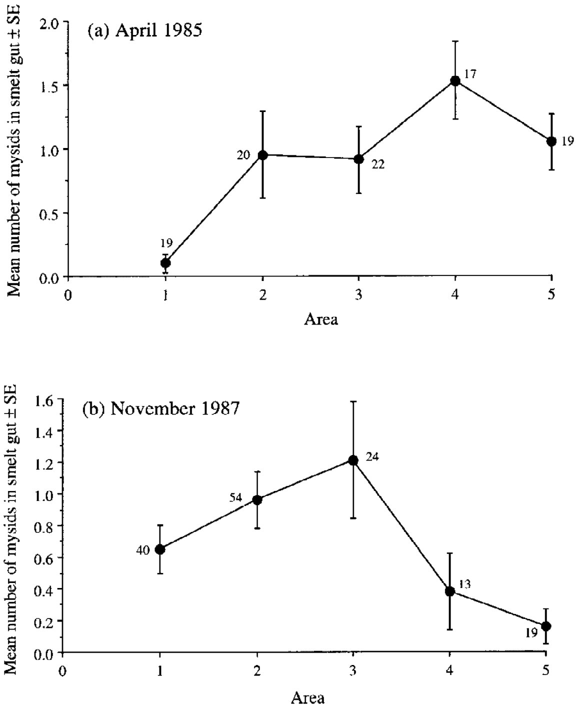

Figure 8. Spatial variations in the mean number of mysids observed in the gut of smelt in spring and fall.

different from what was observed in November when the lowest number of mysids in 1+ smelt gut occurred in the fish captured in area 5.

The areas of Lake Washington where 1+ smelt consumed the most number of mysids in Spring 1985 and Fall 1987 correspond to the areas where the highest densities of mysids were captured in Spring 1991 (Figure 9a) and Fall 1990 (Figure 9b, c), and vice versa. For example, in fall 1987 the highest number of mysids observed in smelt gut occurred in fish captured in areas 2 and 3. This is in consonance with the fact that highest mysid density in fall 1990 occurred in areas 2 and 3 (Figure 9b, c).

Spatial variations in 1+ smelt size and relationship between 1+ smelt size and mysid abundance

The mean sizes of 1+ smelt captured in various areas in summer and fall of odd years (1989 and 1991) when 1+ smelt abundance is high in the lake are presented in Table 2. Significant differences in size were observed in July and December 1989 as well as in October 1991 (ANOVA, P = 0.003), but not in December 1991 (ANOVA, P = 0.313). The smallest mean sizes of fish were observed in area 5 and highest in area 1 or 2 (Table 2).

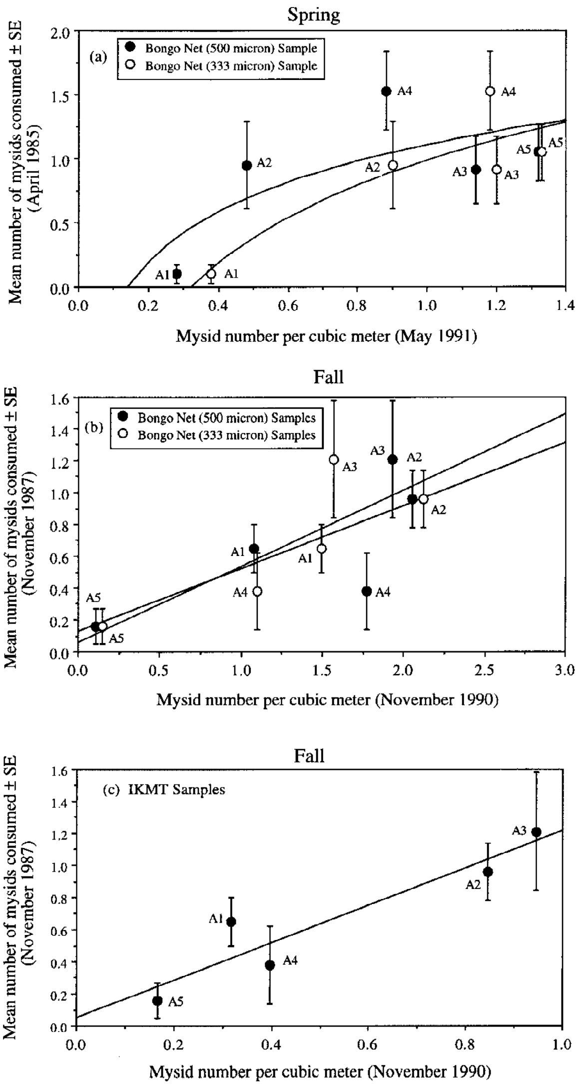

Figure 9. Relationship between the number of mysids consumed by smelt in various areas of Lake Washington and mysid density in spring (Figure 9a) and fall (Figure 9b, c).

There was a positive linear or curvilinear relationship between 1+ smelt size and mysid abundance (Figure 10a–c) except in December 1991 (Figure 10d) when mysid abundance was comparable among the five areas (see Figure 4k).

Spatial variations in mysid size based on IKMT samples

Significant differences were observed in the mean size of mysids captured in various areas of Lake Washington on sampling occasions in summer, spring and fall, but not in winter (Table 3). However, no definite pattern was observed with respect to the differences in mysid size.

There were also significant differences in the mean size of mysids captured at various depths except on sampling occasions in spring (Table 4), perhaps due to the fact that the IKMT failed to capture mysid juveniles released in the lake during this season. Generally, there was a tendency for small mysids to occupy shallow depth strata in July (Table 4).

Discussion

Abundance and night-time horizontal distributions of mysids and smelt

Smelt in Lake Washington mature at the end of two years, then spawn and die (Moulton, 1974). The abundance of 1+ smelt is higher during odd years than during even years (Chigbu & Sibley, 1994b). Details of the reciprocal relationships between 1+ smelt and mysid abundance have been reported elsewhere (Chigbu & Sibley, 1998).

The seasonal differences in the horizontal distributions of mysids and smelt observed in this study suggest that mysids and smelt migrate or are carried by water current from one area to another; sometimes northwards (towards area 1) and sometimes southwards (towards area 5). Horizontal migrations of mysids from nearshore to offshore areas have been reported, especially with respect to temperature (Rudstam et al., 1986; Shea & Makarewicz, 1989). Beach seining in Lake Washington also revealed that *Neomysis* occupy nearshore areas in winter/early spring but move offshore in summer as nearshore temperatures increase (P. Chigbu, personal observation). However, we are not aware of any report on seasonal changes in mysid distribution comparable to what we observed in this study.

There was a tendency for YoY smelt to move northwards following their entry into Lake Washington in spring from the Cedar River, hence their occurrence in high numbers in areas 1 and 2 during the summer. By fall, they had moved southwards from area 1 and remained mainly in area 5 in winter (Figure 4b–d). This northward, and then, southward movement was repeated during the second year of smelt residence in the lake. Since we generally observed similar distribution patterns in the 1988 and 1990 year classes, we believe that smelt distribution in the lake is somewhat predictable. The distribution

Table 2. Spatial variations in mean size of 1+ smelt collected in various areas of Lake Washington. Mean standard Length ± SE (mm) in various months of odd years

Area	Jul. 1989	Dec. 1989	Oct. 1991	Dec. 1991
1	77.2a ± 0.51 (285)*	90.6a ± 1.3 (52)	nd	82.1 ± 0.4 (195)
2	76.2a ± 0.6 (190)	99.0ac ± 4.0 (2)	83.0 ± 1.2 (24)	80.8 ± 0.4 (175)
3	75.7ab ± 1.2 (62)	84.9b ± 0.9 (92)	nd	80.9 ± 0.8 (51)
4	75.3ab ± 1.0 (62)	88.3ac ± 1.3 (63)	79.7b ± 0.8 (83)	81.0 ± 0.7 (96)
5	73.6b ± 0.7 (109)	84.3b ± 0.5 (210)	77.9b ± 0.7 (88)	81.5 ± 0.6 (113)
P-value =	0.0035	0.0001	0.0032	0.3131

*Number of 1+ smelt measured. nd = No data. Mean values with similar letters are not significantly different (ANOVA), Fisher PLSD test, $P<0.05$).

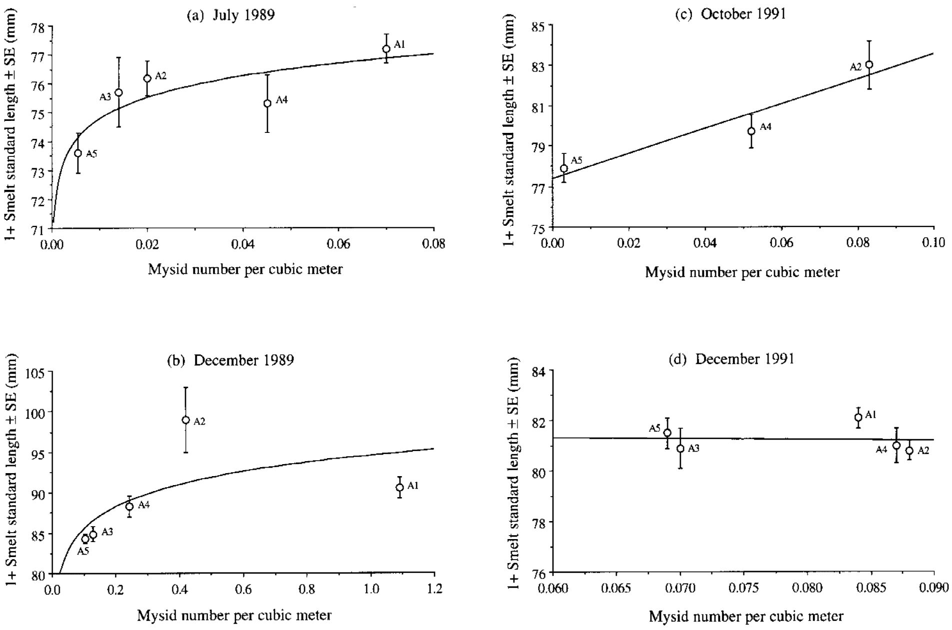

Figure 10. Relationship between 1+ smelt size and mysid density based on samples collected with IKMT.

Table 3. Mean Length of mysids captured in IKMT at night in five areas of Lake Washington

Area	Mean Length ± SE (mm)					
	Jul. 1989	Dec. 1989	Jan. 1990	Apr. 1990	May 1990	Jul. 1990
1	11.1a ± 0.2 (30)*	13.3a ± 0.2 (60)	14.5 ± 0.2 (64)	15.2a ± 0.1 (104)	15.1a ± 0.2 (23)	11.9a ± 0.2 (69)
2	12.9b ± 0.4 (33)	nd	13.7 ± 0.2 (61)	13.9b ± 0.3 (35)	14.1b ± 0.1 (59)	12.1a ± 0.2 (97)
3	12.2ab ± 0.6 (12)	12.4b ± 0.2 (84)	14.1 ± 0.4 (19)	13.9b ± 0.2 (69)	14.1b ± 0.1 (44)	11.8a ± 0.2 (99)
4	11.2a ± 0.3 (61)	nd	nd	nd	14.0b ± 0.1 (30)	11.4b ± 0.1 (98)
5	12.7ab ± 1.1 (5)	13.1ab ± 0.2 (32)	14.1 ± 0.2 (60)	14.1b ± 0.3 (30)	14.2 ± 0.1 (57)	13.0c ± 0.2 (39)
P-value =	0.0009	0.002	0.117	0.0001	0.0008	0.0001

*Number of mysids measured. nd = No data. Mean values bearing similar letters are not significantly different (ANOVA, Fisher PLSD test, $P<0.05$).

pattern is less obvious for the 1989 year class most likely because comparatively few fish were caught.

Migration of 1+ smelt southwards as they mature is understandable because the major tributary (Cedar River) in which smelt spawn is located at the south

Table 4. Mean Length of mysids captured in IKMT at night in various depth strata of Lake Washington

Depth (m)	Mysid Mean Length ± SE (mm)					
	Jul. 1989	Dec. 1989	Jan. 1990	Apr. 1990	May 1990	Jul. 1990
8	11.1a ± 0.2 (80)*	12.6a ± 0.2 (68)	13.9a ± 0.2 (62)	14.3 ± 0.2 (90)	14.1 ± 0.1 (96)	11.7a ± 0.1 (169)
15	11.5a ± 0.4 (31)	nd	14.4a ± 0.5 (14)	14.4 ± 0.3 (38)	13.9 ± 0.1 (34)	12.0ac ± 0.2 (81)
22	13.5b ± 0.5 (8)	nd	13.3ab ± 0.7 (13)	14.7 ± 0.4 (27)	14.3 ± 0.2 (19)	12.2bc ± 0.2 (84)
30	13.0b ± 0.8 (9)	13.2b ± 0.2 (84)	14.5ac ± 0.2 (62)	14.9 ± 0.2 (53)	14.5 ± 0.1 (56)	11.5a ± 0.3 (26)
35	nd	nd	13.4ab ± 0.4 (27)	nd	nd	12.6ac ± 0.3 (7)
50	14.5b ± 0.4 (12)	12.5ab ± 0.3 (24)	14.5abc ± 0.3 (26)	14.2 ± 0.3 (30)	14.3 ± 0.3 (7)	12.5bc ± 0.3 (35)
P-value =	0.0001	0.021	0.039	0.228	0.132	0.016

*Number of mysids measured. nd = No data. Mean values with similar letters are not significantly different (ANOVA, Fisher PLSD test, $P<0.05$).

end of the lake (Martz et al., 1996; Moulton, 1970). The non-spawning migration of YoY smelt also southwards during fall and winter (Figure 4), as well as migration of 1+ smelt northwards during spring and summer is more difficult to explain. Nevertheless, it is interesting to note that the pattern of horizontal distribution of smelt in this study is similar to that described for juvenile sockeye salmon (*Oncorhynchus nerka*) in Lake Washington (Woodey, 1972). Considering seasonal changes in wind directions on Lake Washington, Woodey (1972) and Traynor (1973) concluded that 'wind-induced currents in the surface layers of Lake Washington' might be responsible for the observed distribution of juvenile sockeye salmon. If this is true, the seasonal patterns in smelt distribution may also be largely due to water currents in Lake Washington.

If wind-induced currents in the surface waters due to southerly winds in spring and early summer (Traynor, 1973) also exerted a similar influence on the distribution of mysids, one would expect a northward distribution of mysids in spring, and southward distribution in fall as was noted for 1+ smelt, but this was not so. Mysids swim actively, so avoidance of predation by planktivorous fish, particularly longfin smelt, coupled with local prey depletion by predators, might be an additional influence on *Neomysis* distribution.

Seasonal changes in mysid distribution in this study suggest that *Neomysis* could cover a distance of about 35 km (the length of Lake Washington) in 1–2 months. This is not an unreasonable distance if we assume the maximum swimming speed of *Neomysis* to be about 0.8 m min^{-1},a value estimated for a related species *Mysis relicta* during diel vertical migration (Beeton, 1960; Levy, 1991).

Predation intensity of smelt on mysids is predicted to be higher during summer and fall of odd- than even years (Chigbu, 1993). In this study, mysid horizontal distribution in December 1989 was similar to that in October 1991, but differed from that of November 1990. Since 1+ smelt abundance in the lake was about 6.5 X (December 1989) and 12.8 X (December 1991) higher than in November 1990, it is plausible to hypothesize that mysids occur in relatively large numbers in the central basin of the lake (areas 2 and 3) mainly during the seasons and years when 1+ smelt abundance is quite low in the lake (Figure 3g, h). Thus, 1+ smelt abundance and distribution seem to influence mysid distribution.

In turn, mysid abundance and distribution affected smelt feeding and growth as indicated by: (1) the observed differences in the number of mysids consumed by smelt in different areas of the lake in spring 1985 and fall 1987, (2) the differences in mean size of 1+ smelt captured in various areas of the lake, and (3) the positive relationship between mysid abundance and smelt size during summer and fall of odd years when 1+ smelt abundance is high in Lake Washington. It is notable that the similarity in the sizes of 1+ smelt caught from the five areas in December 1991 agrees with the uniform distribution of mysids in December 1991 (Figure 4k). These pieces of evidence, though not surprising, support the hypothesis that intraspecific competition occurs among 1+ smelt during odd years, and give us confidence to reject the notion that the distribution patterns for smelt and mysids observed in this study are spurious.

The observed spatial differences in mysid mean size showed no consistent significant relationship to mysid or 1+ smelt density, probably because mysids undergo extensive horizontal movement resulting in constant mixing of populations in various areas of the lake. The occurrence of small mysids in shallow depths of the lake is consistent with observations made by other researchers (Murtaugh, 1981c; Rudstam et al., 1989).

Night-time depth distributions of mysids and smelt, and their spatial association

Mysids in Lake Washington occupied mainly shallow depth strata (8–15 m) in area 3 during all seasons. In the early spring, the thermocline in Lake Washington is weakly developed and shallow (5–10 m). From June to November, the lake is strongly stratified, with the thermocline occurring between 10 and 26 m (Traynor, 1973; Murtaugh, 1981c, W.T. Edmondson, Department of Zoology, University of Washington, personal communication), whereas from December to March, the lake is homothermal. Data presented here indicate that *N. mercedis* concentrated mainly in the epilimnion or near the thermocline region when the lake was well stratified. Studies on *Mysis relicta* vertical distribution (Nero & Davies, 1982; Lehman et al., 1990) showed that there was a preference for the thermocline region. Lehman et al. (1990) observed that when the thermocline is weakly developed (June 1985 and 1986), *M. relicta* were either uniformly distributed throughout the water column or were concentrated in the deeper layers of the lake. In contrast, we observed *N. mercedis* in shallower (8 m) than deeper (> 15 m) strata during spring (April to June).

The depth distribution patterns of mysids in this study are different from observations made previously by Murtaugh (1981c) in Lake Washington. His night-time hauls with epibenthic dredge in May, July and September revealed peak mysid abundance just above the sediments. This may be because his samples were collected at a shallower station (20 m) than our stations (> 30 m).

Mysid migration into the epilimnion depends on the steepness of the temperature gradient at the metalimnion. Summarizing studies on *M. relicta* vertical distribution, Beeton & Bowers (1982) indicated that temperature gradients of about 2 °C per meter can inhibit migration of *M. relicta* into the epilimnion. Factors such as magnitude of light intensity and depth of plankton distribution were also reported as being important in the distribution and extent of mysid vertical migration. Cooper et al. (1992) however, captured *N. mercedis* in summer (September) mainly in the epilimnion of British Columbia Lakes, at temperatures of up to 20 °C, and suggested that *N. mercedis* probably tolerates higher temperatures and light intensity than *M. relicta*.

The seasonal patterns of depth distribution, especially during spring and summer, and diel vertical migration of smelt are similar to those of *N. mercedis*. During the day, both smelt and mysids are distributed close to the lake bottom (Murtaugh, 1981c; Beauchamp et al., 1992; P. Chigbu, unpublished data), whereas at night they are captured in comparatively large numbers in the water column from spring to fall. Moreover, their horizontal distributions in summer and winter are somewhat similar. Thus positive correlations in their abundance were observed in summer and spring but negative or poor correlations in fall and winter respectively (see Table 1). This considerable overlap in space and time increases risk of mysid predation by smelt. It is not surprising therefore, that 1+ smelt fed heavily on mysids, particularly, from dusk till midnight (Dryfoos, 1965). Since 1+ smelt are important predators of *Neomysis* and *Daphnia* (Dryfoos, 1965; Chigbu & Sibley, 1994a; 1998) and *Neomysis*, important predators of *Daphnia* (Murtaugh, 1981a, b, c, 1983; Chigbu & Sibley, 1994c) the seasonal variations in the abundance of mysids and 1+ smelt in different areas of the lake have important implications with regard to qualitative and quantitative impacts on their prey.

A noteworthy feature is that during the seasons that mysids are largest in size (e.g. winter and spring) and are therefore more vulnerable to predation, 1+ smelt are either smaller in size relative to other seasons, hence have reduced predation impact on mysids, or they are larger in size but relatively low in abundance and are approaching their spawning time, when predation intensity on mysids is also low (Chigbu, 1993). It may be therefore, that predation by smelt helps to shape the evolution of mysid life history.

Unlike other populations of longfin smelt in Washington State, U.S.A., which are anadromous, the Lake Washington population is land-locked. It is not known how the population became established in the lake. Edmondson & Abella (1988) speculated that smelt became trapped in the Cedar River-Lake Washington drainage in 1916 following the construction of the Lake Washington ship canal. An alternative explanation was that the fish were introduced into the system in late 1950s. Although sampling was conducted in Lake Washington, it was not until 1959 that smelt were caught in the lake (see Schultz & DeLacy, 1935; Dryfoos, 1965) supporting the notion that smelt was introduced into the lake recently. Before smelt became established, the major predators of mysids in the lake were prickly sculpin (*Cottus asper*) and pelagic sculpin (*Cottus aleuticus*) based on feeding habits and population abundance studies (Ikusemiju, 1975; Rickard, 1978). During this period, mysids were quite abundant relative to the present level. With an increase in smelt (a species with a similar pattern of vertical migration) abundance, the effectiveness of diel vertical migration as a predator avoidance strategy decreased due to high spatial overlap between mysids and smelt, hence mysid population density declined and has remained lower than the early 1960s level (Chigbu & Sibley, 1998). It will take a much longer time period before *Neomysis* can evolve an efficient strategy for minimizing mortality due to predation by smelt.

The spatial association of *Neomysis* and smelt was highest in late spring and summer, mainly due to the concentration of a large number of mysids and smelt in the shallow layers of the lake. Poor or negative correlations in their abundance in winter and fall respectively, resulted from differences in their horizontal distribution in fall, and depth distribution in winter. It is likely that the poor correlation between mysid and 1+ smelt abundance in 1990 was because very few 1+ smelt were caught.

We have demonstrated that *N. mercedis* and 1+ smelt show distinct variations in seasonal distributions which determine the extent of their spatial overlap. Because of much overlap in time and space, especially during summer, *N. mercedis* in Lake Washington face a high risk of predation by smelt. This piece of information is in agreement with the hypothesis that longfin smelt control mysid abundance in the lake. However, the overall differences in the spatial distribution of 1+ smelt and mysids in fall and winter may be sufficient to prevent smelt from driving mysids to extinction in the lake.

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