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Relationship between abundance, growth, egg size and fecundity in a landlocked population of longfin smelt, *Spirinchus thaleichthys*

P. Chigbu and T. H. Sibley

School of Fisheries WH-10, University of Washington, Seattle,
WA 98195, U.S.A.

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Sixteen year-classes of longfin smelt, *Spirinchus thaleichthys*, show a consistent pattern of alternating year-class strength between even (strong) and odd (weak) years. A recent (1989) odd year-class grew as well as, if not better than, the late 1960s odd year-classes. However, fish in the even year-classes (1988 and 1990) were significantly smaller in size then the 1966 and 1968 cohorts. Associated with this reduction in growth of the even year-class fish is a decline in fecundity. Fecundity of the odd year-classes of smelt was also smaller than in the early 1960s. Mean egg diameter and gonadosomatic index were not statistically different between 1988 and 1989 year-classes but the relative fecundity was higher for the 1988 year-class than for 1989, suggesting a higher reproductive investment in the even year-class. Reduction in growth and associated reproductive traits is considered to result from a reduction in the abundance of mysids, a preferred prey species.

Key words: reproductive traits; Lake Washington; density–dependence; Osmeridae; mysids.

I. INTRODUCTION

Fish populations may alter their growth rates and fecundity in response to environmental variability (see Nikolskii, 1969; Munkittrick & Dixon, 1989; Wootton, 1990). Hence, understanding the relationship between fish fecundity and body size is important for accurately calculating the potential number of eggs a fish may spawn.

Although the fecundity of land-locked smelts (Osmeridae) varies strikingly between species (Table I), little is known about intra- and interpopulation differences in reproductive traits. Differences in egg size and numbers may be related to the fact that both traits usually increase with fish size (Bagenal, 1978; DeMartini, 1990, 1991; L'Abee-Lund & Hindar, 1990). However, there may also be evolutionary changes in life history traits driven by environmental factors (Stearns, 1976; Wootton, 1990). According to life history theory (Stearns, 1976), there should be a trade-off between egg number and egg size such that in habitats where juvenile mortality rates are high due to density-dependent effects, fecundity will be sacrificed for egg size (Wootton, 1990).

Longfin smelt, *Spirinchus thaleichthys* (Ayres) is an anadromous species distributed from San Francisco Bay to central Alaska (Hart, 1980). However, the population in Lake Washington (Seattle, Washington, U.S.A.) is one of the two land-locked populations in North America, the other being in Harrison Lake, British Columbia.

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The longfin smelt, *S. thaleichthys*, population in Lake Washington exhibits a regular variation in abundance; the even year-class is more abundant than the odd year-class (Moulton, 1970, 1974; Eggers *et al.*, 1978). Furthermore, 1+ smelt abundance for the even year-class increased from less than 1×10^6 in the early 1960s to $2–6 \times 10^6$ during the 1980s (Eggers *et al.*, 1978; J. Ames, Washington State Department of Fisheries, personal communication; Chigbu, 1993). In contrast, the odd year-class has remained at less than 1 million and may have declined in abundance.

Previous studies by Moulton (1974) and Eggers *et al.* (1978) showed that the large year-classes of 1966, 1968 and 1970 had smaller fish than 1967, 1969 and 1971, respectively. Although smelt grew at a slower rate in late 1960s than they did in early 1960s when mysids were more abundant in Lake Washington, no evidence of density-dependent growth was observed from 1972 to 1975 (Eggers *et al.*, 1978).

Dryfoos (1965) and Moulton (1970) noted that smelt spawn at 2 years, from January to April in streams that flow into Lake Washington and that few, if any, survive after spawning. Therefore the odd and even year spawning populations are essentially reproductively isolated. Dryfoos (1965) observed that the fecundity varied from 9621 to 23 624 (mean 18 104) for fish ranging in size from 108 to 126 mm. Although it was apparent that fish were smaller in the 1962 year-class than the 1963 year-class, no attempt was made to compare numbers of eggs produced by the two populations. It is not known, therefore, if there were differences in the reproductive traits of smelt for the even and odd year-classes or if there has been any relationship between smelt fecundity and changes in the Lake Washington environment.

The objectives of this study were to evaluate the relationships between year-class strength, growth and some reproductive traits of smelt. First, available information on growth of the 1988, 1989 and 1990 year-class will be compared to determine if there is compensatory growth in the smelt population. Second, fecundity of recent year-classes is compared with the early 1960s when smelt abundance was comparatively low. Finally, we compare fecundity, egg size and gonadosomatic index (GSI) of smelt for odd and even year-classes to determine if they are different.

II. MATERIALS AND METHODS

ESTIMATION OF FISH ABUNDANCE

Data collected by several workers (Dryfoos, 1965; Moulton, 1974; Thorne & Dawson, 1976, 1977; Dawson & Thorne, 1978; Drew & Thorne, 1979; J. Ames, personal communication) to estimate smelt abundance in Lake Washington from the early 1960s to the late 1980s were compiled. The principal gear used for capturing the fish was a 3 m Isaacs-Kidd midwater trawl (IKMT) with a trawling duration of approximately 10 min at 5 knots. In the 1960s, fish were caught at night in several areas of the lake but sampling was irregular. More regular samples have been collected annually during winter or spring since the mid-1970s by the University of Washington, Fisheries Research Institute (FRI) or the Washington State Department of Fisheries (WDF). Relative abundance of smelt year-classes is expressed as mean catch per unit effort (cpue). Mean cpue = total number of fish captured in a year divided by the total number of trawls.

Table I. Fecundity of landlocked smelt populations*

Species	Locality	Fish length (mm)	Age (years) at first maturity	Fecundity (eggs/fish) (1000)	Source
Osmerus eperlanus	Rjgrod Lake (Poland)	74–101	1–2	4·1–9	Czeczuga (1959)
O. eperlanus	Syam Ozera (Poland)	108–157	2	7·5–20·0	Sterligova (1979)
O. mordax	Lake Superior	185–224	3	22·3–40·9	Bailey (1964)
O. mordax	Lake Erie	97–132	—	5·5–15·3	Nsembukya-Katuramu *et al.* (1981)
Spirinchus thaleichthys	Harrison Lake (British Columbia)	46–61	2	0·535–2·43	Dryfoos (1965)
S. thaleichthys	Lake Washington	108 126	2	16·16–22·21	Dryfoos (1965)

*Modified from Nellbring 1989.

DETERMINATION OF SIZE AT AGE

From July 1989 to February 1992 we collected smelt at approximately 2-month intervals. All fish caught were measured (± 0·1 mm) and weighed (± 0·01 g). The size of fish during their last 9–10 months in the lake was then compared with similar information obtained by previous investigators (Traynor, 1973; Moulton, 1974; Eggers *et al.*, 1978). We adopted the convention of Dryfoos (1965) to designate the age of smelt. Smelt larvae caught in April were designated as age 1 (month), the time when the majority enter the lake; majority of smelt spawn at 24 months of age. Henceforth, all fish ages are given in months unless stated otherwise.

DETERMINATION OF FECUNDITY

Number of eggs per fish was estimated by a wet weight method (Dryfoos, 1965) using smelt that were caught in mid-water trawls during the winter of 1990 and 1991 and showed no indication of previous spawning. Fish were measured and weighed prior to estimating fecundity. The females used for the estimates represent the smallest to the largest individuals present each year. Both ovaries were dissected out and eggs separated from the ovarian membrane in 10% formalin solution, which was then filtered off. The eggs were rinsed with water and excess water was removed using absorbent paper. The entire sample was weighed and one to three subsamples of the eggs were weighed and counted. Egg numbers of subsamples ranged from 273 to 2677. Five replicate subsamples of one fish measuring 113 mm (24·13 g) gave mean absolute fecundity ± 1 S.D. of 16 045 ± 351; the coefficient of variation was 2·19%. For individual fish the total number of eggs per fish was estimated from egg number per known weight of a subsample and total weight of ovaries.

MEASUREMENT OF EGG SIZE AND DETERMINATION OF GONADOSOMATIC INDEX

Diameters of about 20 randomly-selected individual eggs from each fish were measured using an ocular micrometer, under a binocular dissecting microscope. The GSI and relative fecundity (egg counts per unit weight) were calculated for eviscerated fish (Bagenal, 1978). GSI is given as:

$$\text{GSI} = 100\ \text{TEW}/(\text{TW} - \text{TEW})$$

$$\text{and relative fecundity} = \text{number of eggs}/(\text{TW} - \text{TEW})$$

where TEW = total egg weight (g); TW = total body weight (g).

III. RESULTS

FISH ABUNDANCE

There is a regular variation in the abundance of even and odd year-classes of smelt (Fig. 1). The even year-class is consistently more abundant than the odd year-class. Generally, the abundance of smelt has increased from low levels in the early 1960s to a relatively high level in the 1980s. The cpue data for 1963/1964 were for age 4 (months) fish, and 1966/1967, for age 9 (months) fish (see Moulton, 1974). Those of 1975–1978 and 1981–1988 were generally for age 13/14 (months) fish. Thus, the cpue data for the 1966 year-class does not necessarily reflect a very high fish abundance compared with the 1980s, because during the winter/spring when the samples were collected in the 1970s and 1980s, a large percentage of smelt reside in the nearshore areas (Beauchamp, 1987).

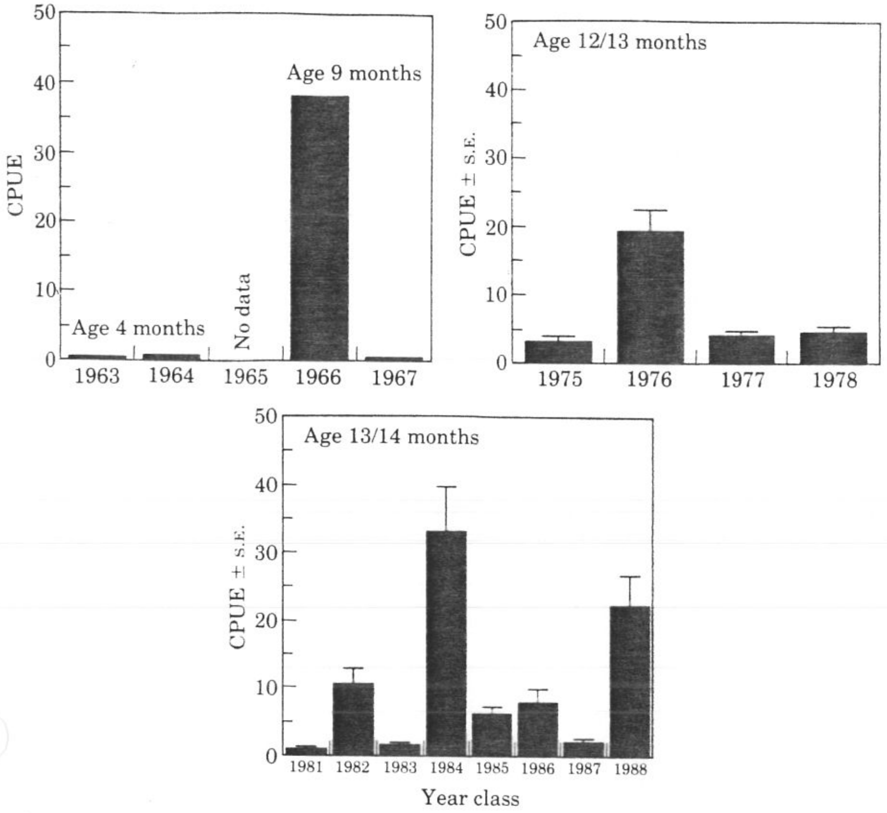

FIG. 1. Mean cpue for smelt collected in Lake Washington. Data for 1960s are from Moulton (1970, 1974), 1970s from FRI reports (e.g. Thorne & Dawson, 1976, 1977; Dawson & Thorne, 1978) and 1980s from WDF.

SIZE AT AGE FOR EVEN AND ODD YEAR CLASSES OF SMELT

Length–frequency analysis was used to separate 1989 and 1990 cohorts. This showed a bimodal distribution with no overlap. After spawning in winter/spring the mature smelt disappear from the lake leaving only one year-class (Fig. 2). Mean length at age for the 1988 and 1990 year-classes of smelt was smaller than for the 1966 and 1968 year-classes (Fig. 3). In contrast, the size at age for the odd year-class of 1989 was comparable to the 1969 and larger than the 1967 year-class (Fig. 3).

A direct comparison of recent year-classes shows that the 1989 year-class was consistently larger than the 1988 and 1990 year-classes (Fig. 4) at approximately the same ages.

FECUNDITY

Fecundity of smelt (Fig. 5) has declined significantly (one-way ANOVA, $P<0{\cdot}0001$) from the 1960s year-classes to the 1980s year-classes. Furthermore, fecundity for the 1989 year-class (YC) was higher than for the 1988 YC (Scheffé-*F*-test, $P<0{\cdot}05$). The mean values were 18 105 ± 1410 S.E. (1960s), 11 795 ± 495 S.E. (1989 YC) and 8310 ± 519 S.E. (1988 YC). When adjusted for size (absolute fecundity/standard length) a significant difference was also

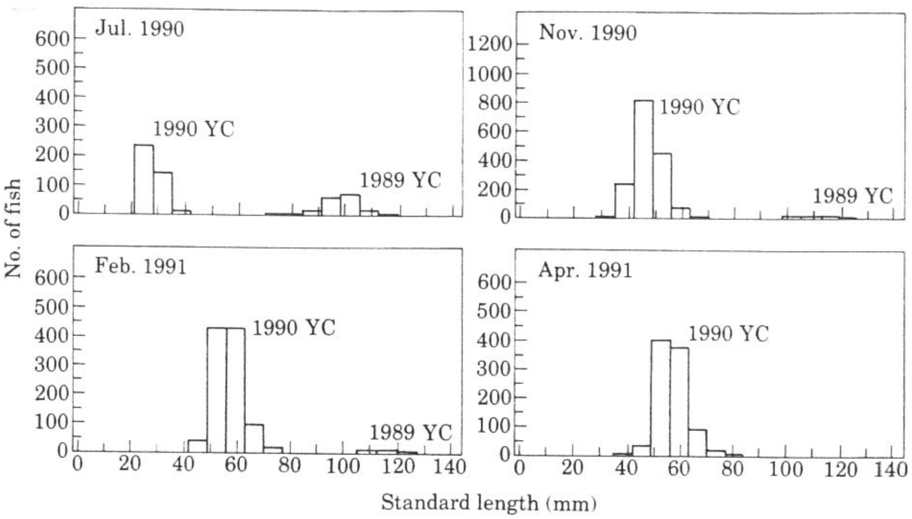

FIG. 2. Length distribution of smelt collected in different months showing 1989 and 1990 cohorts.

observed (ANOVA, $P<0{\cdot}0001$); the 1960s data (mean 155 ± 12 S.E.) were higher (Fisher PLSD test, $P<0{\cdot}0001$) than the 1988 YC (mean=90 ± 5 S.E.) and 1989 YC (109 ± 4 S.E.) but $P=0{\cdot}07$ for a direct comparison of the 1988 YC and 1989 YC. A statistically significant positive linear relationship was observed between female standard length and number of eggs per fish for the 1988 YC ($P<0{\cdot}05$), but not for the 1989 YC ($P=0{\cdot}164$). The equation describing absolute fecundity (AF) in relation to standard length (S.L.) for the 1988 YC is:

$$\mathrm{AF} = -15\,886 + 262\ \mathrm{S.L.},\quad P<0{\cdot}05,\quad r^2=0{\cdot}40.$$

Relative fecundity of the 1988 year-class was higher than the 1989 year-class (t-test, $P<0{\cdot}0001$). However, relative fecundity showed no trend with length for either year-class. The mean and S.E. was 1499 ± 144 ($n=11$) and 911 ± 34 ($n=11$) for 1988 and 1989 year-classes respectively.

EGG SIZE

Mean egg size (MES) was not significantly different (t-test, d.f.=18, $P=0{\cdot}110$) between the 1988 (mean and S.E.=0·83 mm ± 0·02, $n=10$) and 1989 (mean and S.E.=0·89 mm ± 0·03, $n=10$) year-classes. However, egg size distribution differed between the two year-classes. We observed no significant relationship between egg size and fish length for the 1988 year-class but mean egg size increased significantly with fish size (Fig. 6) for the 1989 year-class as indicated below:

$$\mathrm{MES}=0{\cdot}28+0{\cdot}01\ \mathrm{S.L.},\quad P=0{\cdot}30,\quad r^2=0{\cdot}13\ \text{(1988 YC)}$$

$$\mathrm{MES}=-1{\cdot}28+0{\cdot}02\ \mathrm{S.L.},\quad P<0{\cdot}01,\quad r^2=0{\cdot}59\ \text{(1989 YC)}$$

where MES=mean egg diameter (mm); S.L.= standard length (mm).

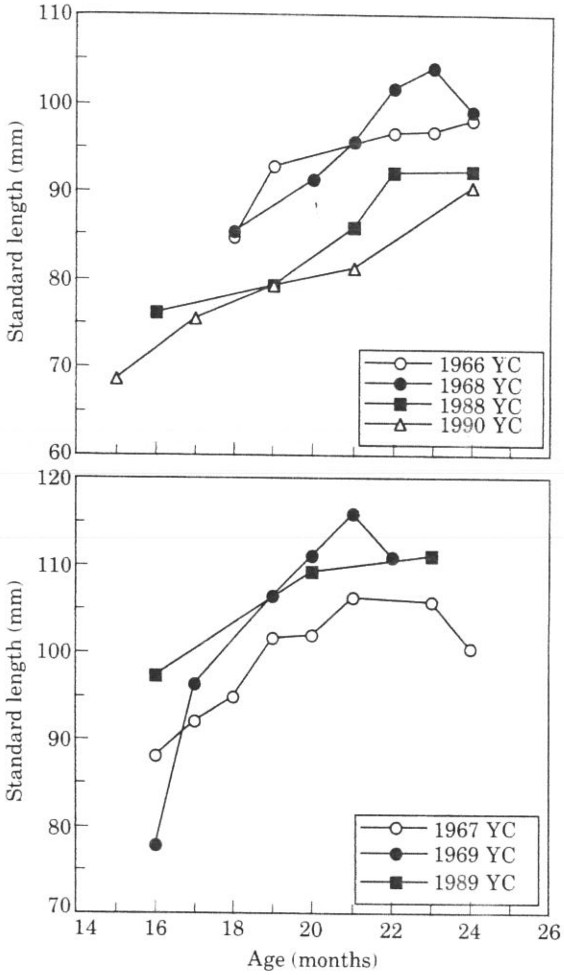

FIG. 3. Mean standard length at age (months) for the even (above) and odd (below) year class (YC) smelt between 1960s and 1980s/1990s. Data for the 1966–1969 year classes are from Moulton (1974).

EGG WEIGHT AND GONADOSOMATIC INDEX

Total weight of eggs increased with fish size (Fig. 7). The relationship is described by the following equations:

$$\mathrm{TEW} = -12{\cdot}19 + 0{\cdot}16\ \text{S.L. for 1988 year-class},\ P<0{\cdot}05,\ r^2=0{\cdot}55.$$

$$\mathrm{TEW} = -38{\cdot}26 + 0{\cdot}40\ \text{S.L. for 1989 year-class},\ P<0{\cdot}001,\ r^2=0{\cdot}75.$$

where TEW=total egg wet weight (g); S.L.=standard length (mm).

We did not find any significant difference in the GSI for 1988 and 1989 year-classes (t-test, $P=0{\cdot}16$); though values obtained were higher for 1988 year-class (mean and S.E.$=40{\cdot}24 \pm 3{\cdot}44$, $n=8$) than for 1989 year-class (mean and S.E.$=33{\cdot}59 \pm 2{\cdot}96$, $n=10$). For each year-class, GSI increased with standard

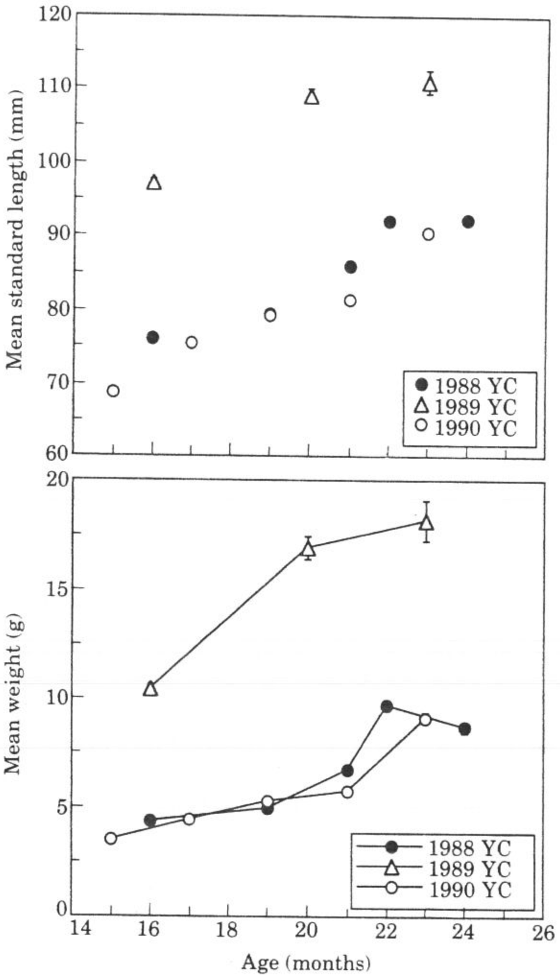

FIG. 4. Mean standard length (above) and mean weight (below) at age (months) for the even (1988 and 1990) and the odd (1989) year class smelt. Error bars are standard error of the means.

length (S.L.) of smelt (Fig. 7), however, the relationship was statistically significant only for the 1989 year-class:

$$\mathrm{GSI} = -165{\cdot}0 + 1{\cdot}84\ \mathrm{S.L.},\ P<0{\cdot}05,\ r^2=0{\cdot}52\ (1989\ \mathrm{YC})$$

$$\mathrm{GSI} = -54{\cdot}9 + 1{\cdot}04\ \mathrm{S.L.},\ P=0{\cdot}19,\ r^2=0{\cdot}25\ (1988\ \mathrm{YC}).$$

IV. DISCUSSION

The cyclic variation in the recruitment of smelt, first reported by Moulton (1970, 1974) and observed in this study, may be rare in smelt populations (but see Henderson & Nepszy, 1989) but has been reported for a number of other fish species (Hamrin & Persson, 1986; Perrow *et al.*, 1990). Probable causes of such oscillations include cannibalism, interspecific density-dependent predation, and intraspecific asymmetrical competition (Ricker, 1962; Hamrin & Persson, 1986;

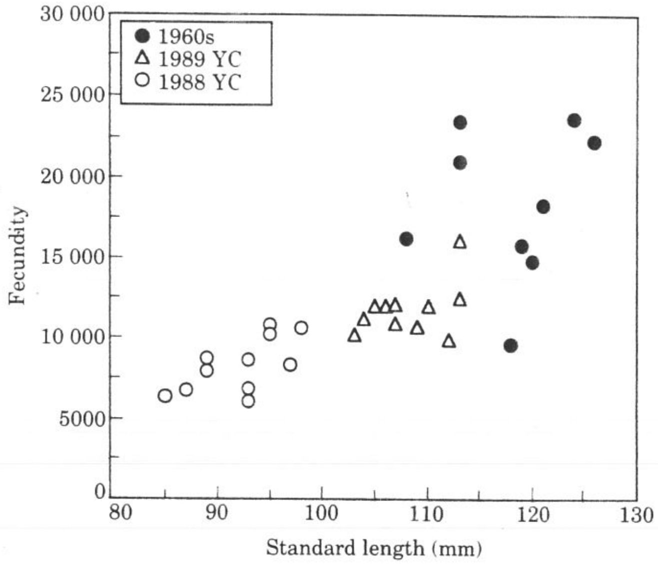

FIG. 5. Relationship between absolute fecundity and standard length of smelt. Fecundity data for the 1960s are from Dryfoos (1965).

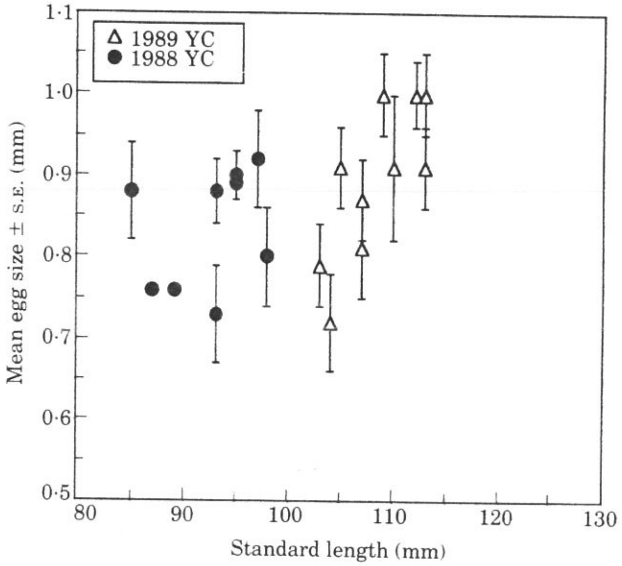

FIG. 6. Relationship between mean egg size and standard length of smelt (below) for the 1988 and 1989 year classes.

Henderson & Nepszy, 1989). Although some workers have reported cannibalism in smelt (Sterligova, 1979; Ivanova, 1982; Evans & Loftus, 1987), no cannibalism has been observed in the Lake Washington smelt population.

quawfish, *Ptychocheilus oregonensis*, (Richardson), rainbow trout, *Oncorhynchus mykiss* (Walbaum), and cutthroat trout, *O. clarki* (Richardson) prey substantially on smelt (Olney, 1975; Beauchamp, 1987, 1990; Beauchamp *et al.*,

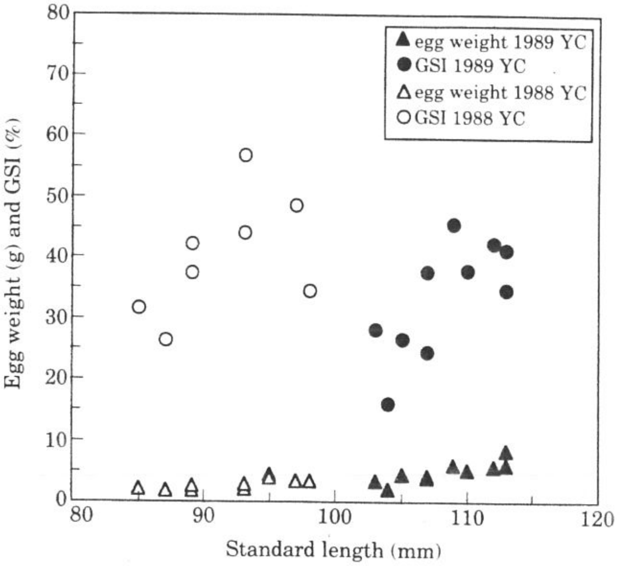

FIG. 7. Relationship between smelt standard length and total egg weight and gonadosomatic index (GSI).

1992). Mortality estimates for odd-YC of smelt are higher than for the even-YC indicating a depensatory mortality (Chigbu, 1993). This should exacerbate the differences in abundance between even and odd-YC (Fig. 1). Depensatory mortality however, does not appear to be responsible for initiating the odd–even year cycle. The cycle was not readily apparent during Dryfoos' (1965) study (Fig. 1) but an extremely successful YC occurred in 1966 (Moulton, 1970). It is important to mention that in the early 1960s, when the lake was polluted with sewage effluents, a large percentage (average = 39%) of smelt possessed structural deformities, the cause of which was not determined (Dryfoos, 1965). The prevalence of these deformities varied from YC to YC. As sewage diversion progressed, the fraction of smelt with deformities declined (Moulton, 1970) and eventually disappeared. If smelt suffered high mortalities due to the skeletal abnormalities and the even YC benefited from the sewage diversion more than the odd YC, it may partly explain how the even–odd year cycle began. According to Dryfoos (1965, Table 13) the incidence of deformities in 1961 (45%) and 1962 (47%) YC was similar, but the incidence in 1963 YC (33%) was twice as high as in 1964 YC (16%). If the 1964 YC had high survival because of the reduced numbers of deformities, it could have produced the large YC observed in 1966.

Fish growth commonly varies inversely with population abundance. Moulton (1970, 1974) hypothesized that reduction in smelt size in Lake Washington from the early to late 1960s was due to a decrease in mysid abundance, which consequently increased intra- and interspecific competition for food. Smelt abundance (even YC) has generally increased since the late 1960s while *Neomysis* abundance has remained relatively low (Chigbu, 1993). This may contribute to further reduction in the size of the even YC fish due to severe intraspecific competition for the scarce mysids. Smelt still prey on mysids but compared with 1960s diet information (Dryfoos, 1965), there is at least a 50% reduction in the number of mysids ingested (Chigbu & Sibley, 1992). Therefore, the mean weight of stomach contents has also declined, even though smelt feed more on microcrustaceans and amphipods. The population abundance of the odd YC of smelt has not increased conspicuously since 1963; compared with the even YC there is less intraspecific competition for large-sized prey. This is supported by the fact that their growth has remained as high as or higher than the odd YC in late 1960s.

Factors affecting growth of fish include the quantity and size of prey (Kerr, 1971; Boisclair & Leggett, 1989; Miller *et al.*, 1990). As fish grow, the type of prey consumed changes and the size of prey increases (Werner & Gilliam, 1984). Failure to find prey of appropriate size often results in stunting (Mittelbach, 1983; Mills *et al.*, 1989*a*, *b*). Comparing rainbow smelt, *Osmerus mordax* (Mitchill), diet and size in several lakes, Evans & Loftus (1987) observed that the relative growth efficiency increased with size of prey consumed. Mysids are ' preferred ' prey of smelt (see Evans & Loftus, 1987) and may enhance growth. Ivanova (1988), citing Arkhiptseva (1977), stated that consumption of large relict crustaceans in the first and second year of life maintained smelt growth rate in low productivity lakes. In bodies of water where mysid abundance increased, an improvement in fish growth was noted (Sokolova, 1991). Reduction of mysid abundance with a concomitant increase in the size at which smelt begin to feed mysids (Chigbu, 1993) might have contributed to the reduction in smelt growth in Lake Washington. Although *Daphnia* are also a preferred prey, less energy might be acquired per unit time spent foraging on microcrustaceans than when mysids were abundant in the lake in the early 1960s. Optimal foraging theory (Mittelbach, 1983) predicts that such a change would reduce growth rate.

The increase in smelt abundance, reduction of mysid density and a consequent decrease in smelt growth seem responsible for the reduction in smelt fecundity. Other studies have shown an inverse relationship between fish density, ration size, growth and fecundity. Deacon & Keast (1987) noted that pumpkinseed sunfish, *Lepomis gibbosus* (L.), ate less and became smaller in an environment where preferred prey were scarce. Cryer *et al.* (1986) and Perrow *et al.* (1990) found a reduction in fecundity of roach, (*Rutilus rutilus* L.), populations when their growth rate was low. Similarly, Weeks & Quattro (1991) observed that growth of a clonal *Poeciliopsis monacha-lucida*, a diploid hybridigenetic ' hemiclone ', decreased with increased population density and food limitation.

The significant difference in the fecundity of the odd and even YC, which may be due to the difference in the mean size of individuals belonging to the two YC or to genetic differences among the YC, indicates that estimates of reproductive potential cannot be based on only one YC. Both relative fecundity and GSI indicate that the even YC (1988), with higher density and lower food resources, invested comparatively more energy into reproduction (Shatunovskiy, 1988) than the 1989 YC. This result conflicts with Ivanova (1988) who observed that slow growing smelt, *Osmerus eperlanus* (L.), were smaller in size and had smaller absolute and relative fecundity than fast growing smelt. Similarly, Weeks & Quattro (1991) found that clutch size per female weight was not affected by variation in diet amount or population density. Moodie (1986) found evidence that female reproductive effort and growth in brook stickleback, *Culaea inconstans* (Kirtland), was inversely related to density. However, Wootton (1977) showed that female sticklebacks, *Gasterosteus aculeatus* (L.), apportioned a higher percentage of acquired energy into egg production when given low rations. Altukhov & Yerastova (1974) reported that relative fecundity of *O. eperlanus* in Kandalaksha Bay, White Sea did not vary substantially for females of the same age. However, we find much higher relative fecundity for the 1988 YC than for 1989, although there is no clear trend with size for either YC. The number of eggs per female in the Lake Washington smelt population remains among the highest reported for land-locked smelt populations (see Table I).

Some evidence indicates that egg size is not affected much by food level (Wootton, 1973; Weeks & Quattro, 1991). Smelt eggs are very small. Dryfoos (1965) obtained mean egg size of 1·0 mm for females with the largest eggs and those with partially spent eggs. Some individuals were found with eggs as small as 0·65 mm. Significant reductions in the size of eggs would result in small larvae, which are predicted to suffer higher mortality (Ware, 1975). It is therefore not surprising that mean egg size of smelt has not changed remarkably since the 1960s as the mean egg diameter in this study also lies between 0·65–1·00 mm. Indeed, the relative variability in egg size is only 10% of the variability in fecundity. Mean egg diameter in 1989 was larger than 1988 although these differences may not be significant (P=0·11). It is more important to compare the patterns of egg size within each year. In 1988, when the population abundance is high, there is only a weak relationship between egg size and fish length although there is a strong relationship between fecundity and length. In contrast the 1989 YC had a strong relationship between length and egg size but a weaker relationship between length and fecundity. In several studies, egg size increased with female size (e.g. DeMartini, 1990, 1991) as data for 1989 YC indicate. However, Bailey (1964) failed to find a relationship between smelt, *O. mordax*, size and egg diameter. In Lake Washington smelt populations it appears that small, perhaps energetically limited, fish increase fecundity rather than egg size whereas larger fish (>100 mm) invest in larger eggs rather than increased fecundity. This is consistent with life history theory if we consider that high fecundity (~10 000 eggs per female) should increase competition among juveniles. It is ironic, however, that in Lake Washington the greatest competition occurs during even years among offspring of small females.

Munkittrick & Dixon (1989) provided a classification scheme for differentiating fish population responses to environmental change on the basis of mean age, fecundity and condition factor of fish. The growth and fecundity responses observed in this study are characteristic of a type IV or V response of fish to environmental change. A type IV response occurs when there is a decline in food availability whereas a type V response is observed when there is a change in food availability such that a niche shift occurs. Both types of response are characterized by: (1) an increase in age at maturity, (2) a decrease in growth rate, (3) a decrease in condition factor, (4) a decrease in fecundity, and (5) a decrease in egg size. In this study, both type IV and V responses seem to have occurred as the decline in the abundance of mysids has resulted in a diet shift to prey such as *Daphnia*, copepods and amphipods. However, no increase in age at maturity occurred during this study and smelt condition factor was not determined.

Rupp & Redmond (1966) transplanted small smelt, *O. mordax*, to new habitats to determine if variation in the population characteristics of smelt was controlled by the environment or the genetic composition of the stock. They found that growth rate and longevity of smelt was virtually controlled by the environment. This study on longfin smelt suggests that the biological characteristics of smelt may be modified by a change in the abundance of an important prey resource. Differences in the growth of even and odd YC fish is most likely related to the difference (five to 15 times) in the abundance of smelt during even and odd years (Beauchamp, 1987). However, we do not have any information concerning the genetic differences between YC.

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