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Changes in Lake Trout Growth Associated with Mysis relicta Establishment: A Retrospective Analysis Using Otoliths

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Abstract.—The establishment of the opossum shrimp *Mysis relicta* in Flathead Lake, Montana, was followed by a dramatic increase in the population of lake trout *Salvelinus namaycush*. Using otoliths, we compared lake trout growth before and after the arrival of *M. relicta*. The widths of annual increments 1–3 were similar, but width generally declined in increments 4–10 after the establishment of *M. relicta*. To calculate body size in the post–*M. relicta* fish, we used the relationship between body length and otolith radius. To retrospectively calculate body length for the pre–*M. relicta* fish (for which we lacked body sizes), we developed a simple empirical correction to account for the conservative nature of otolith growth rate relative to body growth rate.

Mysis relicta (Mysidacea: Mysidae) is a shrimp native to northeastern and north-central North America and northern Eurasia (Dadswell 1974). Fisheries managers introduced *M. relicta* in western North American and Scandinavia (Gregg 1976; Fürst 1981; Lasenby et al. 1986) largely because of the increased growth and sustained abundance of kokanees *Oncorhynchus nerka* after *M. relicta* addition to Kootenay Lake, British Columbia (Sparrow et al. 1964; Northcote 1972). These results generally have not been duplicated elsewhere (Morgan et al. 1978; Beattie and Clancey 1991; Bowles et al. 1991), however, and appear to be related to the particular morphometry and nutrient enrichment of Kootenay Lake (Northcote 1972; Martin and Northcote 1991).

Mysis relicta remain on the bottom during the day and migrate vertically at night (Juday and Birge 1927) to feed, particularly on large cladocerans (Cooper and Goldman 1980; Spencer et al. 1999). The shrimp appear to shuttle a substantial quantity of macro zooplankton production from the pelagic zone to the profundal, and *M. relicta* introductions generally have decreased the abundance of pelagic planktivores while benefiting profundal fishes (Lasenby et al. 1986; Hammar 1988; Bowles et al. 1991; Langeland et al. 1991).

Between 1968 and 1976, *M. relicta* were introduced from Waterton Lake, which is on the eastern side of the continental divide in Montana, into 12 lakes on the western side. Populations were established in at least seven lakes (Crystal, Little Bitterroot, McGregor, Swan, Ashley, Whitefish, and Holland), the latter four of which are upstream of Flathead Lake. By 1981, *M. relicta* had established in Flathead Lake by way of downstream drift (Spencer et al. 1991).

The establishment of *M. relicta* dramatically changed the food web of Flathead Lake. The density of cladocerans and the most abundant copepod declined after *M. relicta* introduction (Spencer et al. 1991, 1999). Lakewide spring gill net monitoring captured 14 times more nonnative lake trout *Salvelinus namaycush* per sinking gill net from 1996 to 1998 than was the average in 1981 and 1983 (because of the small number of lake trout captured in 1981 and 1983, this increase should be considered only approximate). Besides lake trout, only nonnative lake whitefish *Coregonus clupeaformis* showed an obvious increase in the nets. In contrast, the abundance of native bull trout *S. confluentus*, cutthroat trout *O. clarki*, and nonnative kokanees decreased in the nets post *M. relicta* (M. Deleray, Montana Department of Fish, Wildlife and Parks, personal communication). The decreases in bull trout and kokanees are also apparent from redd surveys (Beattie and Clancey 1991; Spencer et al. 1991; Rieman and Myers 1997).

The lake trout expansion in Flathead Lake is remarkable considering the relatively late maturity

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(at >4 years) of this species (Martin and Olver 1980), and the expanded lake trout population appears to be influencing other fishes in the lake. Lake trout have replaced bull trout as the dominant piscivore in Flathead Lake and compete heavily with bull trout in other systems (Donald and Alger 1993). Predation by the expanded lake trout population is also impacting the abundance of fishes in the lake, particularly kokanees (Carty et al. 1997), which have virtually disappeared from the lake despite a substantial stocking effort.

The objective of this study was to examine growth changes in lake trout otoliths associated with *M. relicta* establishment in Flathead Lake by using a sample collected after the introduction of *M. relicta*. We were particularly interested in any insights the growth patterns could provide into causes of the lake trout population expansion. To relate changes in otolith sizes to body lengths for the pre–*M. relicta* fish (for which body sizes were unknown), we developed a simple empirical correction to account for the conservative nature of otolith growth rate relative to body growth rate. We independently validated this procedure with lake trout from nearby Lake McDonald.

Methods

Flathead Lake (47°52′N, 114°04′W) and Lake McDonald (48°35′N, 113°55′W) are deep, oligotrophic lakes of the upper Columbia basin in northwest Montana, Lake McDonald being colder and less productive. These lakes have similar guilds of native and nonnative fishes; however, Lake McDonald remains uninhabited by *M. relicta*. More detailed information on Flathead Lake and its food web is provided in Spencer et al. (1991) and Stanford and Ellis (in press). Lake trout were captured in Flathead Lake with experimental gill nets ranging from 19- to 51-mm-bar mesh from December 1986 to August 1995; they were captured from Lake McDonald in 1991 and 1994. We used 151 fish from Flathead Lake and 14 from Lake McDonald for this analysis. Fish were weighed (g), total length (TL in mm) was determined, and sex was recorded for 117 of the Flathead Lake fish. Otoliths (sagittae) were removed from the fish and stored dry. Otoliths were embedded in epoxy and a transverse section was cut through the primordium. Sections were polished and annual increment widths (μm) were determined along an axis from the primordium to the dorsal margin. All otoliths were read by a single reader using a compound microscope with an image capture system. The first two or three increments were opaque and difficult to read. The incomplete increment was removed from calculations of average increment widths, but not for measurements of total otolith radii.

We compared otolith growth rate pre and post *M. relicta* introduction (hereafter, ''pre'' and ''post,'' respectively) by comparing average otolith increment widths for the first 10 increments. Increments beginning in 1970–1984 were categorized as pre, those after 1984 were considered post. We based this division on the first collection of *M. relicta* in Flathead Lake in 1981 and their low densities from 1981 to 1984 (<3/m²; Spencer et al. 1991).

We used the average otolith radius at annulus and the relationship between TL and otolith radius to calculate TL at annulus pre and post after addressing several biases. We were concerned that the gill nets selectively captured fast-growing young fish, so we compared the increment widths of young fish with the corresponding increment widths from the older fish to evaluate gill net selectivity. Several authors have reported that otolith growth rates are conservative relative to body growth rate (Templeman and Squires 1956; Reznick et al. 1989), so fast-growing fish will have smaller otoliths at a given body size and vice versa. Thus any growth rate differences pre and post would be problematic for the calculated pre TL because the body size versus otolith size relationship was calculated from post fish. To resolve this issue, we quantified the relationship between body and otolith growth rate and accounted for the effect on the calculated pre TL. Body growth rate was calculated as the residuals of the regression of TL versus number of complete increments. Otolith growth rate was calculated as the residuals of the regression of otolith radius versus TL. The relationship between body versus otolith growth rate was determined by regression of the corresponding residuals. The slope of this relationship was multiplied by the difference in the average post and pre otolith radius at each annulus for which the otolith increment data indicated that growth patterns differed pre and post. This correction factor was added to the TL obtained by entering the pre otolith radius at annulus into the post TL versus otolith radius regression. To check this method, we applied the analogous procedure to the Lake McDonald fish, which we expected would have slower growth rates than the Flathead Lake fish.

We examined whether *M. relicta* establishment corresponded to changes in the size of angler-caught fish or changes in diet. We examined trends

in the total lengths of angler-caught lake trout in four year-round creel surveys from 1961 to 1963 (Robbins 1966), 1981–1982 (Graham and Fredenberg 1982), 1992–1993 (Evarts et al. 1994), and 1998–1999 (B. Hansen, Confederated Salish and Kootenai Tribes Tribal Fisheries Program, personal communication). The most important (by weight) diet item for lake trout was described for 1980–1982 (Leathe and Graham 1982); 1986–1988, 1989, and 1996 (Montana Department of Fish, Wildlife and Parks, Dingell-Johnston reports); and 1998–1999 (D. Beauchamp, University of Washington, unpublished). Stomachs were collected throughout the year for 1980–1982, 1986–1988, and 1996. Stomachs from 1989 were collected May to September, whereas the 1998–1999 collection was made from May to June and from October to November 1998 and from March to June 1999. The 1980–1982, 1986–1988, and 1989 collections were primarily from larger fish (>500 mm TL), whereas those from 1996 and 1998–1999 contained similar proportions of smaller (<500 mm) and larger fish. For the 1996 and 1998–1999 collections, we documented the most important diet item for the larger fish only.

Results

The Flathead Lake fish had 1–38 complete increments at capture; those of the Lake McDonald fish ranged from 2 to 15. Student's *t*-tests revealed no significant differences in increment widths between Flathead Lake females and males for all sexed fish in increments 1–10 ($0.055 \le P \le 0.950$). On the basis of similar otolith growth rates between the sexes, we pooled females and males for further analysis.

Our analysis focused on Flathead Lake fish that had 1–22 complete increments. We chose not to use the oldest fish because the sample was small. Fish less than 350 mm TL were captured infrequently, and all fish with 1–3 complete increments were less than 350 mm TL ($n = 31$). We evaluated the selective capture of fast-growing young fish by comparing the first 3 average increment widths for fish with 1–3 complete increments (all of which were post) with the corresponding post increment averages from fish with 4–22 complete increments. This analysis suggested the gill nets selectively captured fast-growing fish with 1 or 2 complete increments (Table 1). On the basis of these findings and the small sample size of fish with 3 complete increments ($n = 4$), we removed fish with 1–3 complete increments from the pre versus post comparison of lake trout growth rate.

TABLE 1.—Mean widths (μm) of annual increments 1–3 for Flathead Lake lake trout with varying numbers of complete increments at capture, with sample sizes in parentheses to evaluate gill-net selectivity. The last row shows the 95% confidence intervals (CI) of the post–*M. relicta* fish with 4–22 complete increments.

Number of complete increments and CI	Annual increment		
	1	2	3
1	567 (13)		
2	510 (14)	244 (14)	
3	520 (4)	204 (4)	153 (4)
CI (4–22 increments)	462–528	204–233	155–171

Using *t*-tests, we compared the average widths of the first 10 increments pre and post with captured fish having 4–22 complete increments. Mean increment widths were significantly smaller for all increments from 4 to 10 except for 5, whereas widths in increments 1–3 were similar (Figure 1; Table 2). Otoliths from the Lake McDonald fish generally grew less than those in fish from Flathead Lake, especially in increment 1 (Table 2).

Partial regressions revealed that the relationship between body size and otolith depended on growth rate. The relationship between body length and the number of complete increments was described for all Flathead Lake fish with 4–10 complete increments as follows: $TL = 226 + 45.0 \cdot I$ ($n = 51$, $R^2 = 0.511$, $P < 0.001$). The relationship between otolith radius and TL was $R = 599 + 1.53 \cdot TL$ ($n = 51$, $R^2 = 0.742$, $P < 0.001$). We used the residuals from these equations as indices of body and otolith growth rate, respectively, yielding the relationship $B = 0.000 - 0.364 \cdot O$ ($n = 51$, $R^2 = 0.222$, $P < 0.001$; Figure 2). To determine whether the relationship between body growth rate and otolith growth rate varied with fish age, we pooled the fish into categories based on the number of complete increments: 4–7 ($n = 22$) and 8–10 ($n = 29$). We then created a multiple regression model of otolith growth rate, increment category, and the interaction to predict body growth rate. We found no significant interaction ($P = 0.853$), indicating that the body growth rate versus otolith growth rate relationship did not vary detectably between groups.

To calculate the pre and post body lengths, we attempted to remove biases that may have been introduced by the conservative nature of otolith relative to body growth rate. We were concerned that the selective capture of fast-growing young fish may have distorted the body size versus otolith size relationship. To reduce this bias, we resam-
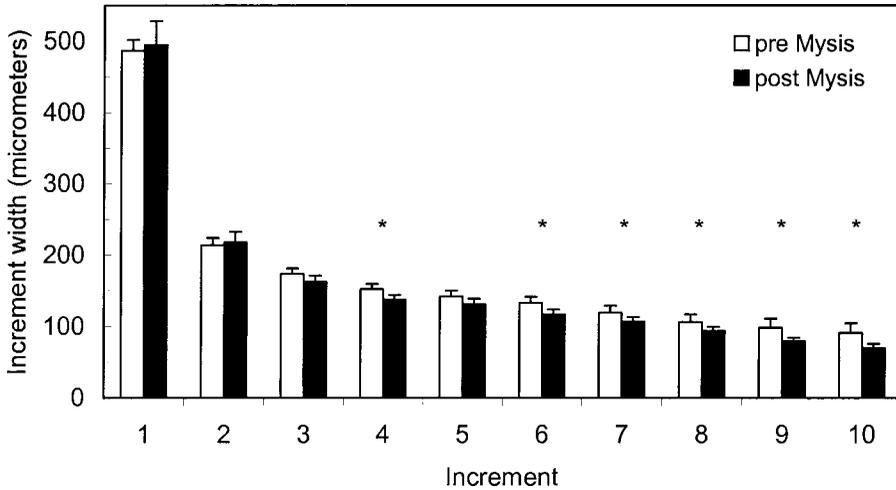
FIGURE 1.—Annual increment widths of lake trout from Flathead Lake before and after the establishment of *M. relicta*. Error bars denote 95% confidence intervals; asterisks denote significant differences between the before and after values ($P < 0.05$).

pled fish having 1–3 complete increments, removing fish if any increment width differed by more than one standard deviation from the corresponding increment mean based on the post fish with 4–22 complete increments. The new pooled mean for increment 1 in fish with 1–3 complete increments ($n = 18$) was 496 μm, increment two in fish with 2–3 complete increments ($n = 10$) was 218 μm, and increment three in fish with 3 complete increments ($n = 3$) was 168 μm. These values were similar to the corresponding average increment widths calculated from the older fish (Table 1). After removing the fast and slow growers, we calculated the overall body length−otolith radius re-

lationship for all fish with 1–22 complete increments; the result was $L = 0.0850 \cdot R + 0.000341 \cdot R^2 - 0.0000000917 \cdot R^3$ ($n = 128$, $R^2 = 0.992$, $P < 0.001$; Figure 3). Because otolith growth rates for the young fish were similar pre and post, we used this equation to calculate TL at annuli 1–3 for both post and pre fish, using the respective average otolith radius at annulus. To generate the post body lengths for annuli 4–10, we calculated the body length versus otolith radius relationship for fish with 4–13 complete increments born in 1982 and later. Thus, 1985 (the first year considered post in this study) is the first date incorporating increment 4 (the first increment

TABLE 2.—Average annual increment width for lake trout from Lake McDonald, Flathead Lake before the establishment of *M. relicta*, and Flathead Lake after the establishment of *M. relicta*, together with sample sizes and *P*-values for *t*-tests of before and after widths of Flathead Lake fish with complete increments 1 to 10.

| Location, sample size, and statistic	Annual increment									
	1	2	3	4	5	6	7	8	9	10
Width (μm)										
McDonald	342	196	169	136	129	101	99	92	82	65
Flathead, preestablishment	487	214	173	152	142	133	119	106	98	91
Flathead, postestablishment	495	218	163	138	131	117	107	94	79	70
Sample size										
McDonald	12	12	12	12	11	9	8	8	6	5
Flathead, preestablishment	87	75	62	52	46	36	28	23	19	18
Flathead, postestablishment	23	35	48	58	58	61	62	65	62	49
P-value, pre- versus postestablishment	0.634	0.657	0.065	0.002	0.062	0.006	0.039	0.029	0.001	0.006
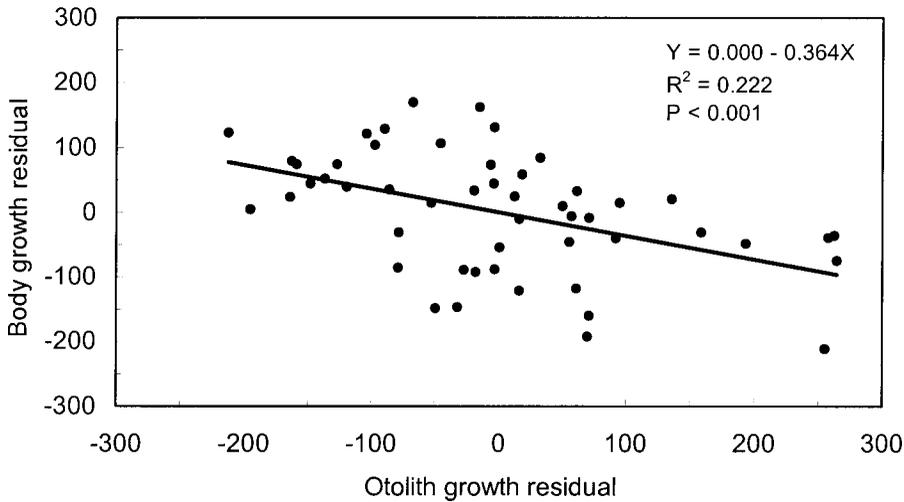
FIGURE 2.—Relationship between body growth rate and otolith growth residuals for Flathead Lake fish with 4–10 complete increments.

where otolith growth rate declined post). The TL versus otolith radius relationship for these fish was TL = −124 + 0.468·R (n = 58, R^2 = 0.773, P < 0.001). This equation was used to generate the average post TL for annuli 4–10 by using the post average otolith radius at annulus. We also used this equation with the average pre otolith radii at annulus to calculate uncorrected pre TLs for annuli 4–10. Because the pre growth rate was generally faster in increments 4–10 and because the body size versus otolith size relationship depended on growth rate, we applied our correction procedure (see methods) to calculate corrected pre body

lengths at annuli 4–10. By accounting for the conservative nature of otolith growth rate relative to body growth rate, the calculated pre body lengths increased, particularly for the older fish (Figure 4).

We tested our correction procedure by using the Lake McDonald fish. The body versus otolith size regression for the Lake McDonald fish with 4–15 complete increments was described by the equation TL = −201 + 0.463·R (n = 12, R^2 = 0.791, P < 0.001). We used this equation and the average radius at annulus to calculate TLs for annuli 4–10. The slow somatic growth rate of the Lake McDonald fish resulted in a body length versus
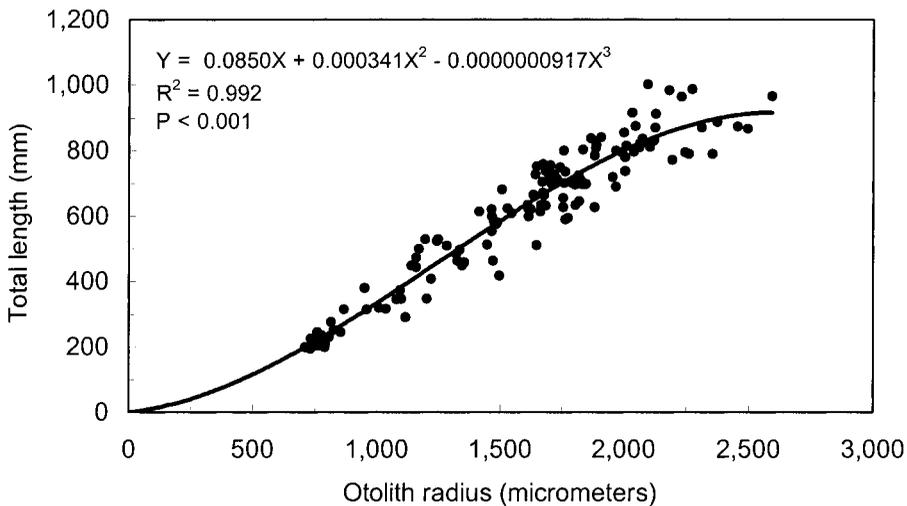

FIGURE 3.—Relationship between body length and otolith radius for Flathead Lake fish with 1–22 complete increments after removal of the fast- and slow-growing fish with 1–3 complete increments.
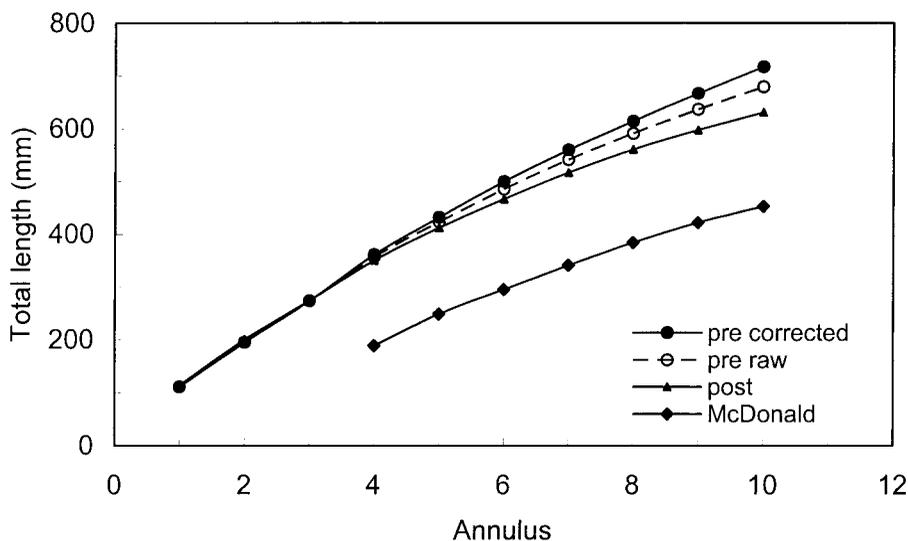
FIGURE 4.—Length at annulus for lake trout from Flathead Lake after (post) the establishment of *M. relicta* and before that establishment (1) without accounting for the conservative nature of the otolith growth rate relative to the body growth rate (pre raw) and (2) after accounting for the conservative nature of the otolith growth rate relative to the body growth rate (pre corrected). Values are also shown for lake trout from Lake McDonald (McDonald).

otolith radius relationship below the 95% confidence interval generated by the post fish in Flathead Lake with 4–13 complete increments. We reasoned that the body length difference between the post and Lake McDonald lines should be approximated by the Lake McDonald otolith radius at annulus minus the corresponding post radius multiplied by the slope of the regression relating

post body growth rate to otolith growth rate. Adding the correction increased the Lake McDonald body lengths to within the 95% confidence interval of the post regression. The slower growth rate of Lake McDonald fish was responsible for the lack of overlap with the post fish for annuli 4 and 5 (Figure 5).

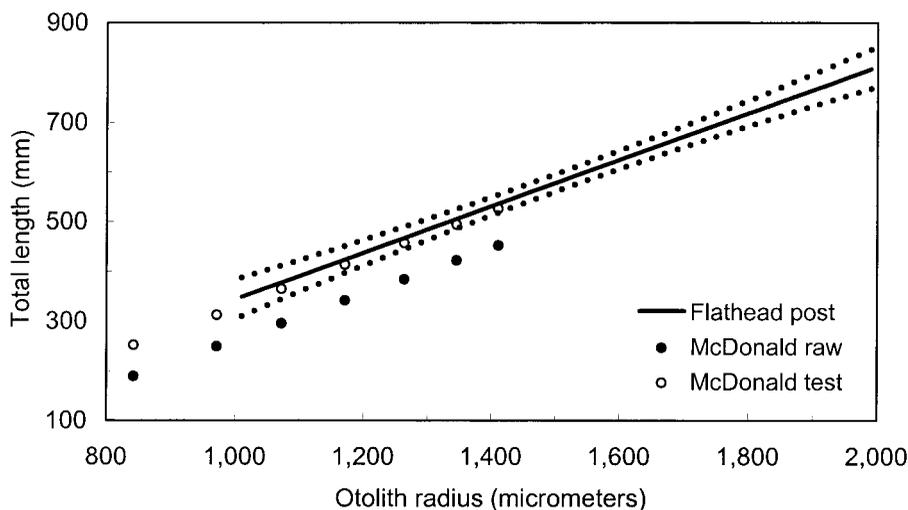The average length of angler-caught lake trout

FIGURE 5.—Body length versus otolith radius for Flathead Lake lake trout after the establishment of *M. relicta* with 95% confidence interval (Flathead post), Lake McDonald lake trout lengths at annulus 4–10 (McDonald raw), and calculated Lake McDonald lake trout lengths to test the correction procedure (McDonald test).
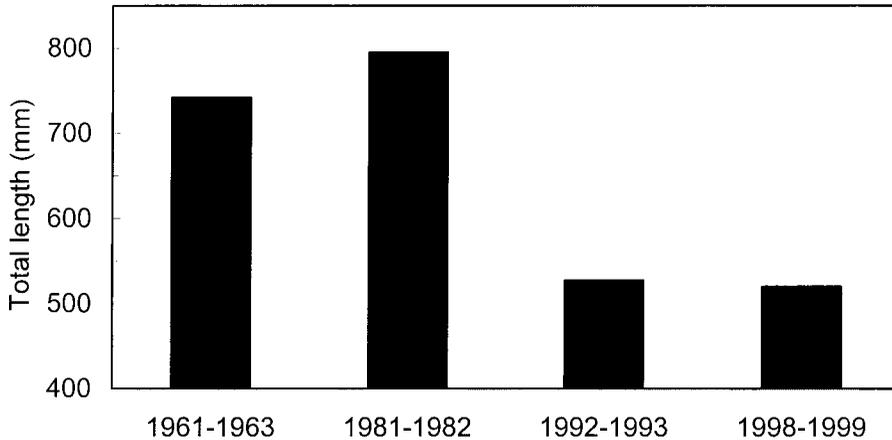
FIGURE 6.—Average length of angler-caught lake trout from Flathead Lake. *Mysis relicta* were first detected in Flathead Lake in 1981 and became abundant in 1985.

declined after the kokanee crash in 1987 (Figure 6). The most important diet item for larger lake trout pre *M. relicta* was kokanees; this was replaced by lake whitefish after the kokanee crash (Table 3).

Discussion

Contrary to our expectations, establishment of *M. relicta* in Flathead Lake did not correspond to detectable growth changes in the first three increments. *Mysis relicta* is an important forage item for immature lake trout, especially the younger fish (Eschmeyer 1956; Griest 1977). We have no diet data for very young lake trout (<200 mm) from Flathead Lake, but fish in the 200–500 mm range make extensive use of *M. relicta* (Beauchamp, unpublished). Positive relationships have been reported between *M. relicta* and growth of the young lake trout in Green Lake, Wisconsin (Hacker, cited by Martin and Olver 1980), and Twin Lakes Reservoir, Colorado (Griest 1977). Several factors may have contributed to our contradictory findings. *Mysis relicta* densities in Flathead Lake are generally low compared with those in other systems (Lasenby 1991; Spencer et al. 1991). Further,

the new forage provided by *M. relicta* may have been offset by increased intraspecific food competition associated with the strong expansion of the lake trout population. Any growth changes that did occur may have been obscured by size-selective mortality, which can be particularly strong for early life stages (Miller et al. 1988; Hambright et al. 1991), or by the opaque and difficult to read early otolith growth.

The reduced growth in the older lake trout post most probably resulted from increased intraspecific competition and changes in the forage fish community after the establishment of *M. relicta*. Before *M. relicta*, kokanees represented an abundant, preferred food source. Kokanees were the most important food item from the 1980–1982 collection. Kokanees remained the dominant food item in the 1986–1988 collection, even though kokanee spawners declined sharply in 1986 and were low in number by 1987 (Spencer et al. 1991). After the kokanee crash, less preferred lake whitefish became the main food item, particularly for the larger lake trout. Bowles et al. (1991) also reported declines in adult lake trout growth (as measured by condition factor) associated with *M. relicta* establishment and kokanee declines in Priest Lake, Idaho.

The reduced adult growth post resulted in a pattern of increasing divergence in the lengths at annulus relative to the pre fish. The shorter average length of angler-caught fish primarily reflects the younger age composition of the post lake trout, and secondarily the reduced growth rate. Declines in the large lake trout fishery (>640 mm) have also been reported in Lake Tahoe after *M. relicta*

TABLE 3.—Date captured, most abundant diet item (by mass), and sample size (*n*) for lake trout (primarily >500 mm total length) captured at Flathead Lake.

Date	Diet item	*n*
1980–1982	Kokanee	15
1986–1988	Kokanee	123
1989	Lake whitefish	282
1996	Lake whitefish	214
1998–1999	Lake whitefish	177

establishment and associated decreases in kokanees (Richards et al. 1991).

The reduced growth in the older fish post strongly suggests that increased growth, survival, or fecundity of adults was not responsible for the population expansion. However, despite the dramatic population increase, growth remained relatively constant in the first three increments, suggesting that the expansion arose from increased survivorship of young fish. The vertical migration of *M. relicta* transfers zooplankton production from the pelagic to the profundal. This food pump may have expanded the area suitable for immature lake trout to feed in, facilitating the population expansion. The presumably abundant spawning habitat in the rocky littoral zone of Flathead Lake and the large average size (i.e., high fecundity) of the lake trout pre appears to have primed the population to expand with the enhanced survival of the young fish.

The lake trout population expansion is a major component of the food web reconfiguration associated with *M. relicta* establishment in Flathead Lake. Although lake trout probably were increasing slowly in abundance since their introduction in 1905 (Spencer et al. 1991), *M. relicta* appears to have facilitated the strong lake trout population expansion through improved survival of the young fish. Apparently, the expanded lake trout population is largely responsible for the kokanee declines in Flathead Lake (Carty et al. 1997), although the decreased populations of large zooplankton also need to be considered (Beattie and Clancey 1991; Spencer et al. 1999). Further, we strongly suspect the lake trout expansion is at least partially responsible for the bull trout declines post. In nearby Swan Lake, which until very recently lacked lake trout, bull trout have become more abundant after *M. relicta* introduction, although this has been confounded with changes in the angling regulations (Rieman and Myers 1997; Baxter et al. 1999). Nevertheless, *M. relicta* alone do not seem to have been detrimental to bull trout in this system. The contrasting bull trout population trends between Swan and Flathead lakes illustrate how multiple species introductions can synergistically reconfigure food webs.

We found that otolith growth rate was conservative relative to body growth, as has been reported by others (Templeman and Squires 1956; Reznick et al. 1989; Lombarte and Lleonart 1993). This was apparent both within the Flathead Lake sample and in the Lake McDonald fish relative to the Flathead Lake fish post *M. relicta*. Accounting

for the conservative growth rate of otoliths relative to body growth rate increased the calculated body lengths at annulus 4 and higher. Applying the analogous procedure to the slow-growing Lake McDonald fish resulted in a body length versus otolith radius relationship similar to that of the Flathead Lake fish, supporting the validity of our approach. Further, the growth difference between the Lake McDonald fish and the Flathead Lake post fish was much greater than the pre and post growth difference. These results illustrate the need to account for the conservative nature of otolith growth rate relative to body growth rate when using otoliths to predict body size (see Morita and Matsuishi 2001). We found no evidence for differences in the body growth rate versus otolith growth rate relationship between the 4–7 or 8–10 complete increment groups. However, if the body growth rate versus otolith growth rates relationship varies with age, we recommend calculating an age-specific correction.

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