Smolting in Steelhead Trout <u>Salmo gairdneri</u> : A Comparative Study of Populations in two Hatcheries and the Trinity River, Northern California, Using Gill Na, K, ATPase Assays.

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A Sea Grant Project

September 1976

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ABSTRACT

Sodium potassium-activated ATPase levels in gill filaments of juvenile steelhead trout were used to assess smolting in both hatchery and wild populations in northern California. In the Trinity River, the peak of the wild steelhead smolt occurred in mid to late May. At the Mad River Hatchery, smolting in yearlings peaked in early April, while at the Trinity Hatchery, smolting in yearlings was asynchronous, with the onset occurring before March 4 and no clear peak in the cycle appearing. Two-year-olds and summer run (Washougal strain) yearlings were also included, but in smaller numbers; asynchronous smolting was also indicated for these two groups. Possible reasons for asynchronous and early smolting are discussed.

INTRODUCTION

The Trinity River drains 2,965 square miles of mountainous terrain in northwestern California (Trinity and Humboldt Counties), and it enters the Klamath River about 42 miles upstream from the Pacific Ocean. Historically the Trinity was noted for its large runs of salmon and steelhead trout. In 1963, the Trinity River Division of the Central Valley project was completed, and export of Trinity River water to the Sacramento Valley was begun. Two dams, Lewiston and Trinity, now block upstream migration of anadromous fish and have resulted in the loss of 109 miles of steelhead habitat in the upper Trinity River system. About twenty-five percent of the drainage area lies above these dams.

The Trinity River Hatchery, situated at the base of Lewiston Dam, was constructed by the U. S. Bureau of Reclamation to compensate for the loss of historic salmon and steelhead spawning and nursery grounds upstream from the dam. The hatchery became operational in 1963. It has an overall capacity to rear 31,000,000 chinook salmon, 4,000,000 coho salmon, and 5,000,000 steelhead. Although most are released as fingerlings, an aggregate of 2,000,000 fish can be reared to yearling size (Hubbell, 1973).

While the numbers of coho and spring-run chinook salmon returning to the hatchery have been increasing, returns of fall-run chinook salmon and steelhead have been poor. The highest number of steelhead returns in the last 10 years was 992 in 1965-66; the low was 67 in 1970-71, and in 1975-76, 175 returned (Hubbell, 1973; Hubbell, pers. comm.). This contrasts to a mean yearly estimate of 10,000 spawning steelhead above Lewiston before the dams were constructed (Hubbell, 1973).

Although there are a number of hypotheses seeking to account for the poor hatchery returns, one of the most intriguing is that an alteration of smolting intensity, duration, and/or time of onset has been brought on by changes in water temperatures. A number of recent studies have shown that high water temperatures greatly reduce the duration of smolting (Adams et al., 1973, 1976; Wagner, 1974a). In addition Wagner (1974a) has recently shown that although changing photoperiod controls the onset of smolting, the temperatures at which fish are reared prior to smolting have pronounced effects on the migratory behavior associated with smolting.

The influence of temperature on smolting was of particular interest to us because the low stream flows in the Trinity River resulting from export of water to the Central Valley have resulted in warmer river temperatures earlier in the spring runoff season. Furthermore, temperatures at the Trinity River Hatchery do not duplicate the downstream river pattern. Hatchery water originates from deep levels of Trinity Lake (Claire Engle Reservoir) and passes through the smaller Lewiston Reservoir, from which it is taken to supply the Trinity Hatchery. Since the time for water to pass through Lewiston Reservoir is normally only a few days, hatchery water temperatures have reflected the cold and relatively constant temperatures typical of deep lake water and, consequently, have been much cooler in summer and fall than would be expected in rivers in this geographical region. (The recent acquisition of a skimmer to draw surface water for the hatchery from Lewiston Reservoir may help alleviate this condition in the future).

The recent development of a reliable biochemical technique has provided a tool for quantifying the smolting process. Zaugg and McLain (1970, 1972) measured Na^+, K^+-activated adenosinetriphosphatase (Na,K, ATPase) in coho and chinook salmon and steelhead trout gills and showed that the enzyme increased as smolting progressed, then decreased again to parr levels if fish were retained in fresh water. Although survival in sea water is possible before the parr-smolt transformation (Wagner, 1974b), Zaugg and Wagner (1973) showed the activity of gill Na,K, ATPase was increased in fish exhibiting migratory behavior. Thus in terms of management, the measurement of Na,K, ATPase in steelhead gills may be of more significance as an indicator of migratory behavior than of salt water survivability. Migratory behavior, in turn, may be the most important consideration in deciding when to release juveniles from hatcheries.

The work reported here was designed to assess the period and intensity of steelhead smolting in the Trinity Hatchery and River. We hoped to discover whether aberrations in smolting period and/or intensity were at least partially responsible for poor adult returns to the hatchery and reduced runs in the river. Steelhead were selected over salmon as the study species because a marking program at the hatchery made possible the differentiation of wild and hatchery fish in the river. A second hatchery, Mad River near Arcata, California, with a more normal water temperature regime, gave us another hatchery population for additional comparisons.

METHODS

Sampling

Fish were taken for ATPase assays at weekly intervals from early March, 1976, until mid May or early June, 1976, depending on availability of the stocks being sampled. In general, samples consisted of 6 specimens of Trinity strain yearlings from the hatchery, 6 wild Trinity River smolts, 6 Mad River strain yearlings from the Mad River Hatchery, 3 Trinity Hatchery 2-year-olds, and 3 summer run (Washougal strain) yearlings from each hatchery. In a typical sample of 6 yearlings, 3 in the 15 to 20 cm size range and 3 over 20 cm were selected in order to minimize the effect of size on ATPase activity. With the exception of two 14.5 cm wild (Trinity River) smolts, all fish assayed were 15 cm or greater.

The California Department of Fish and Game maintained two netting stations for downstream migrants during the course of the study. One was located at the confluence of the Trinity and Klamath Rivers (Weitchpec) and was the source of most of the wild Trinity strain smolts used. The other, 62 miles upstream at Big Bar, provided a few wild strain fish in March and also supplied fish released upstream during the season by the Trinity Hatchery.

ATPase assay

Gill filaments were dissected from the arches at the sampling stations and immediately homogenized with a rotating teflon pestle homogenizer in a 0° C solution with the following composition: .020 M N-2-hydroxyethylpiperazine-N'-2-ethanesulfonic acid (HEPES), .005 M EDTA, .005 M $MgCl_2$, .25 M sucrose, and 0.2% Triton X-100 detergent. The pH was adjusted to 7.2 with Tris base. The homogenate was maintained at 0° and assayed either that day or the next. The homogenate does not begin to lose ATPase activity for 48 hours if kept at 0°, but in practice we always did the assays 30 hours or sooner after homogenizing the filaments. A weight to volume ratio of 1 to 20, tissue to homogenizing solution, was used.

The homogenate was centrifuged at 10,000 x g for 20 min at 0°, following which 0.1 ml of the supernatant was used for determination of the Mg^{++}-activated ATPase and 0.1 ml for Na,K, ATPase. Incubation tubes contained 0.2ml of buffer (.020 M $MgCl_2$, .10 M HEPES, Tris base to bring pH to 7.0), 0.10 ml homogenate, 0.20 ml .5 M NaCl/.1 M KCl for Na^+,K^+ ATPase tubes only, and H_2O to reach a volume of 0.9 ml. The reaction was started by adding 0.10 ml of .035 M Tris-ATP[1] after temperature equilibration (28°C). After 15 min, the reaction was stopped by addition of 1.0 ml of 15% trichloroacetic acid. The incubates were centrifuged at 16,000 x g for 15 min, then 1.0 ml was removed from each for determination of inorganic phosphate. The method of Fiske and SubbaRow (1925) was used for phosphate determination.

Protein content of homogenate was done by the method of Lowry et al. (1951), with an appropriate correction for Tris in the homogenizing solution. Enzyme activity is expressed as μ-moles of inorganic phosphate released per hour per mg protein.

RESULTS

Gill Na,K, ATPase activities ranged from a high of 4.6 μ-moles of phosphate x hr^{-1} x mg^{-1} protein in a wild Trinity strain individual to a low of less than 0.1 in a

[1] ATP was prepared by passing di-Na ATP through a Dowex-50 (H^+ form) column and neutralizing with Tris base.

Trinity Hatchery yearling. As a test of our methods, we measured gill ATPase in two large (>16 inches) steelhead which had been adapted to full strength sea water for about 6 months. Values were 5.5 and 3.4. In contrast, three 8 inch Kamloops strain rainbow trout (a non-anadromous strain native to inland areas of the Pacific Northwest) yielded values of .07, .74 and .17. These results verified our techniques, since a number of workers have shown that seawater adaptation alone is an adequate stimulus for development of high gill Na,K, ATPase levels (Zaugg and McLain, 1971; Pfeiler and Kirschner, 1972).

Trinity River - wild strain

Among wild Trinity strain steelhead, gill ATPase development increased weekly to a high mean value of about 3.2 on May 11. A gradual decline followed, but a small sample (3) on June 15, the last sampling date, had a mean value of 3 (fig. 1). By that time, numbers of captured fish at the Weitchpec netting station had declined markedly, and maximum daily water temperatures were exceeding 18° (fig. 2). Table 1 lists numbers of wild strain steelhead captured at Weitchpec during the study. Note that the apparent peak in migration followed peak ATPase activity by 2 to 3 weeks.

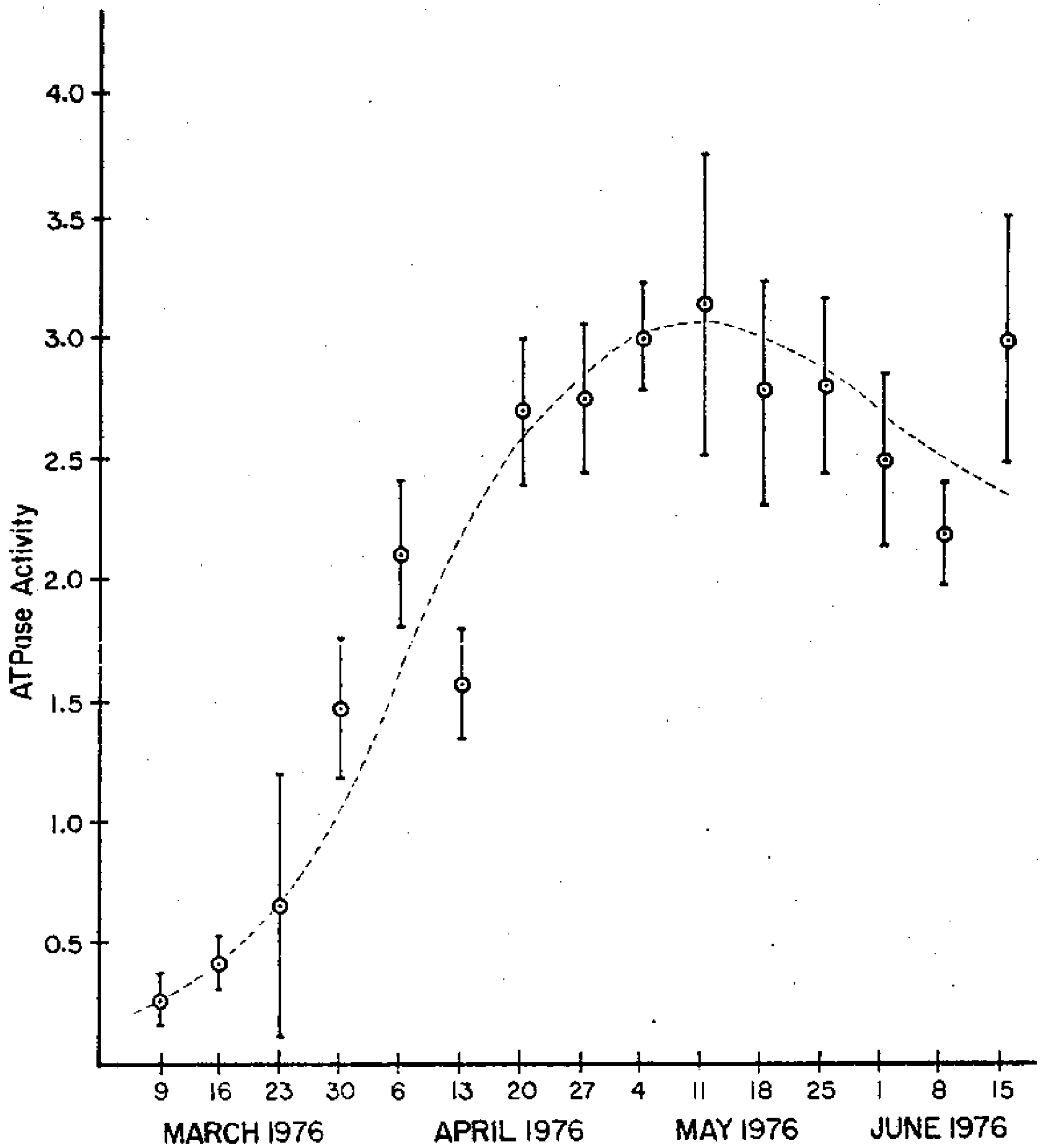

Figure 1. Gill Na,K, ATPase in wild steelhead captured in the Trinity River. Samples taken from March 9 through 23 were from Big Bar, all others were from Weitchpec. ATPase activity is in µ-moles phosphate x hr^{-1} x mg^{-1} protein. Each point represents the mean ± S.E. of single ATPase determinations on each fish in the sample; see Figure 8, appendix, for sample sizes.

Table 1

Weekly totals[1] of wild juvenile steelhead captured in two nets[2] in the Trinity River at Weitchpec, Spring, 1976.

Week ending	Outside channel	Main channel[3]	Total
3-30	17		
4-6	38		
4-13	122		
4-20	130		
4-27	241		
5-4	193		
5-11	212	594	806
5-18	105	671	776
5-25	511	994	1,505
6-1	400	1,125	1,525
6-8	144	444	588
6-15	13	116	129

[1]Preliminary data from William Heubach, Anadromous Fisheries, California Dept. of Fish & Game.
[2]The precise positions of the nets were changed occasionally as river flows changed. The outside net was not fished on May 2 and May 28; estimates based on catches the preceding and following days were used to complete weekly totals.
[3]The main channel net was not fished prior to May 2.

oOo

The netting stations were designed to capture downstream migrants, so ATPase values of Trinity River fish do not represent results of random sampling. Zaugg and Wagner (1973) documented a correlation between gill Na,K, ATPase and migratory behavior, thus we must assume we were selectively sampling fish with high ATPase levels. Nevertheless, the combination of numbers of fish captured

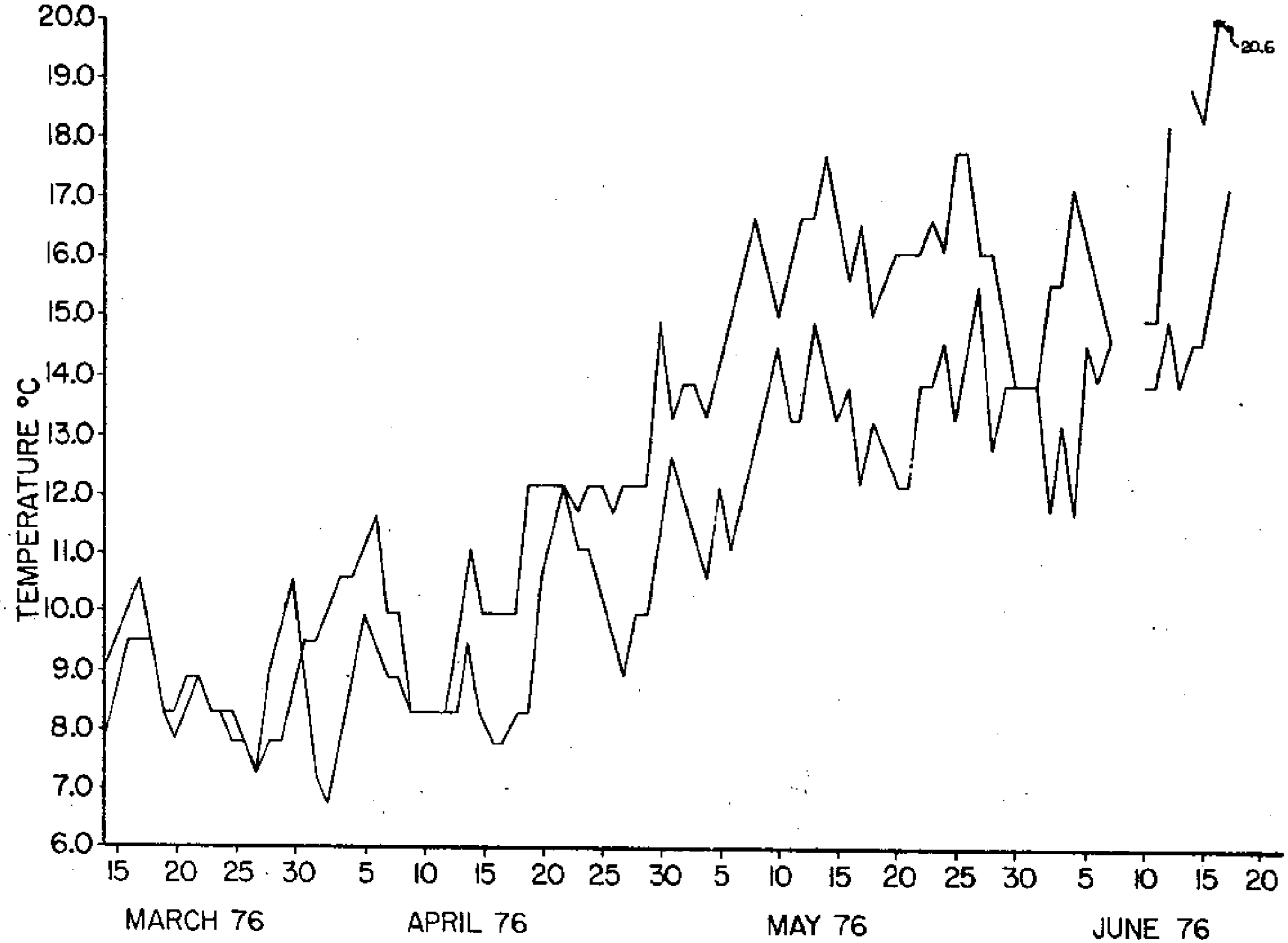

Figure 2. Daily high and low water temperatures of Trinity River at Weitchpec from March 14 to June 17, 1976.

and levels of gill ATPase together give a true picture of the smolting pattern in the river.

Trinity Hatchery yearlings

In contrast to the wild fish, Trinity Hatchery yearlings showed no clear peak in mean ATPase levels during the sampling period (fig. 3). Moderately high enzyme values were already evident in early March, when the first samples were taken, and a decline became apparent in April. By mid May, low ATPase values indicated that smolting had apparently ended, possibly as a consequence of high hatchery water temperatures (>15°C beginning the first week in May [fig. 4]). In support of the possible effects of water temperatures, Trinity Hatchery yearlings released in April and captured subsequently at the Big Bar netting station had moderate ATPase levels well into May (fig. 9, appendix).

Mad River yearlings

Mad River strain yearlings reached an apparent peak of smolting on 5 April (fig. 5), 5 weeks before the Trinity River peak. As was the case at the Trinity Hatchery, gill ATPase activity was moderately high at the beginning of the study on March 1. But it continued to increase to a mean of 2.7, declined to values between 1.5 and 2.0, then decreased abruptly in mid May as water temperatures reached daily highs in excess of 18° (fig. 6).

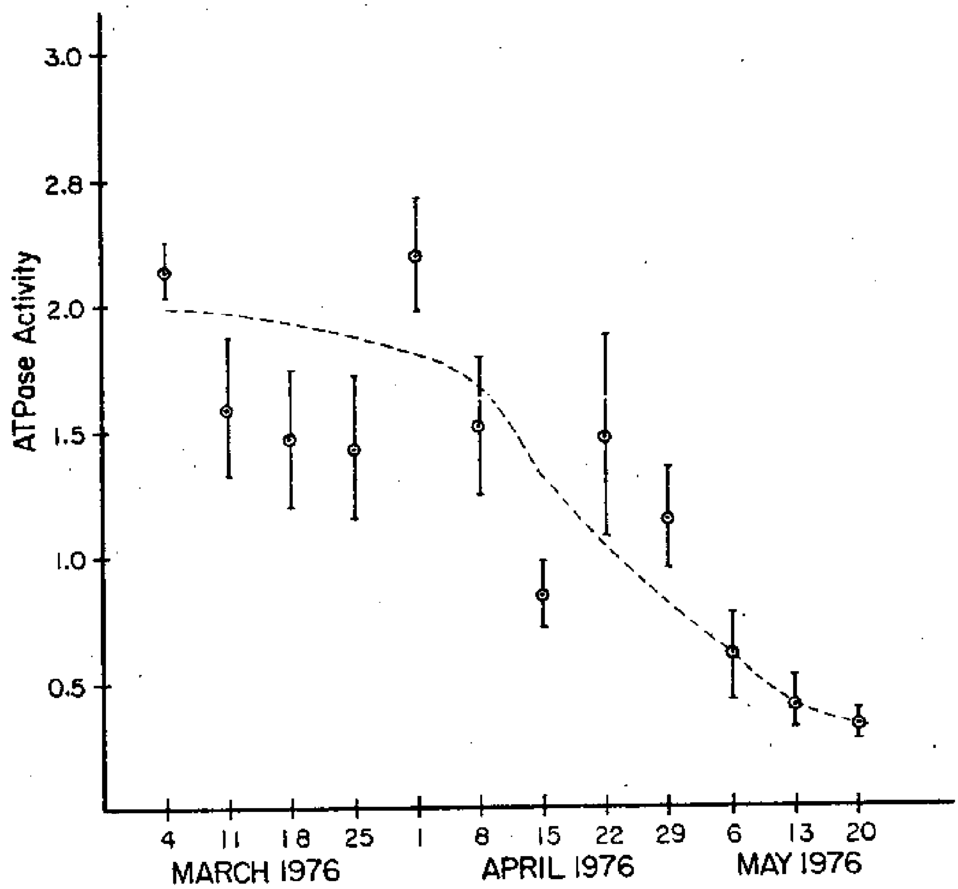

Figure 3. Gill Na,K, ATPase activity in Trinity strain yearlings at the Trinity Hatchery. Each point represents the mean ± S.E. of individual determinations. See Figure 9, appendix, for number of fish per sample.

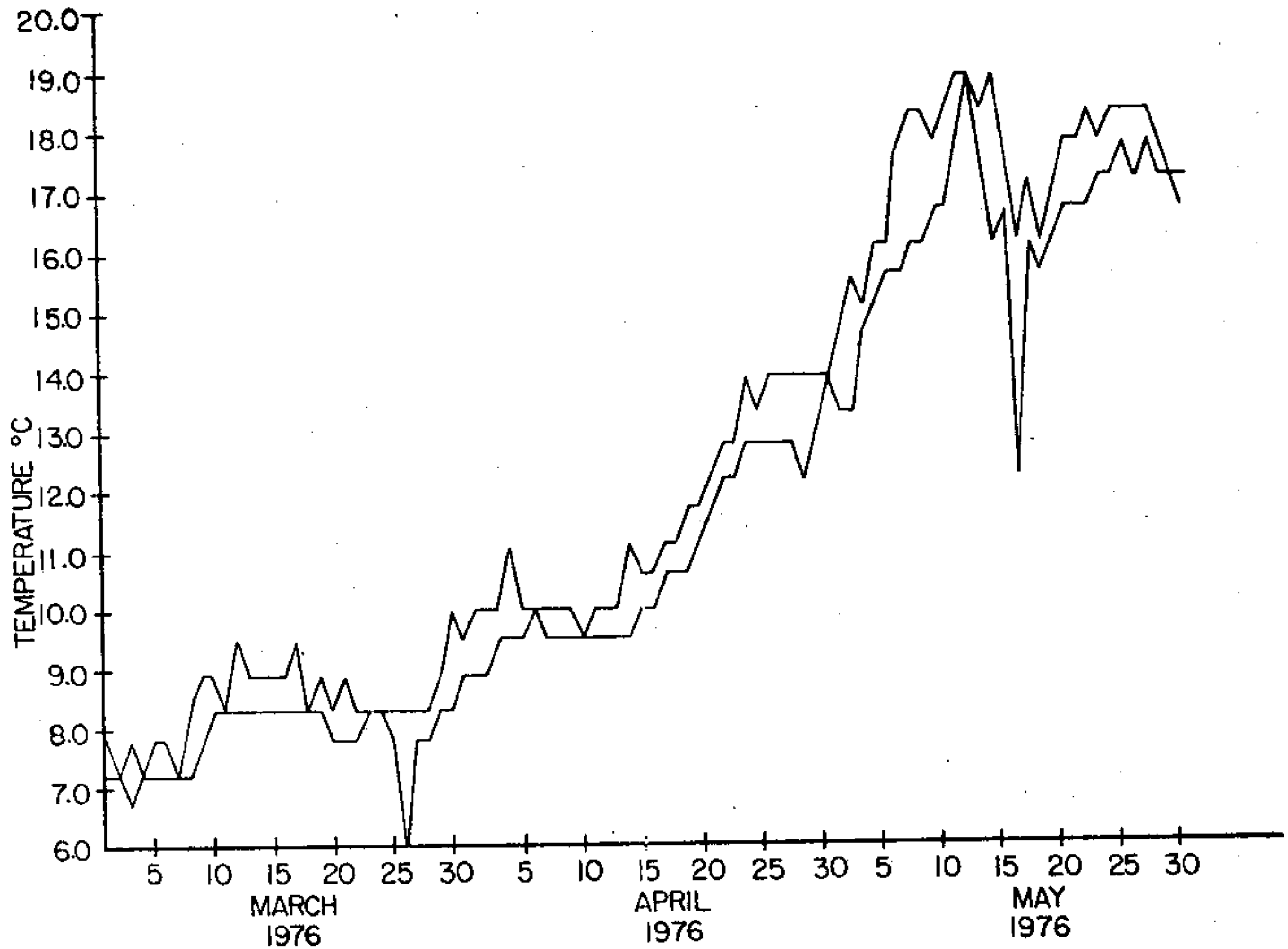

Figure 4. Daily high and low water temperatures at the Trinity Hatchery from March 1 to May 31, 1976.

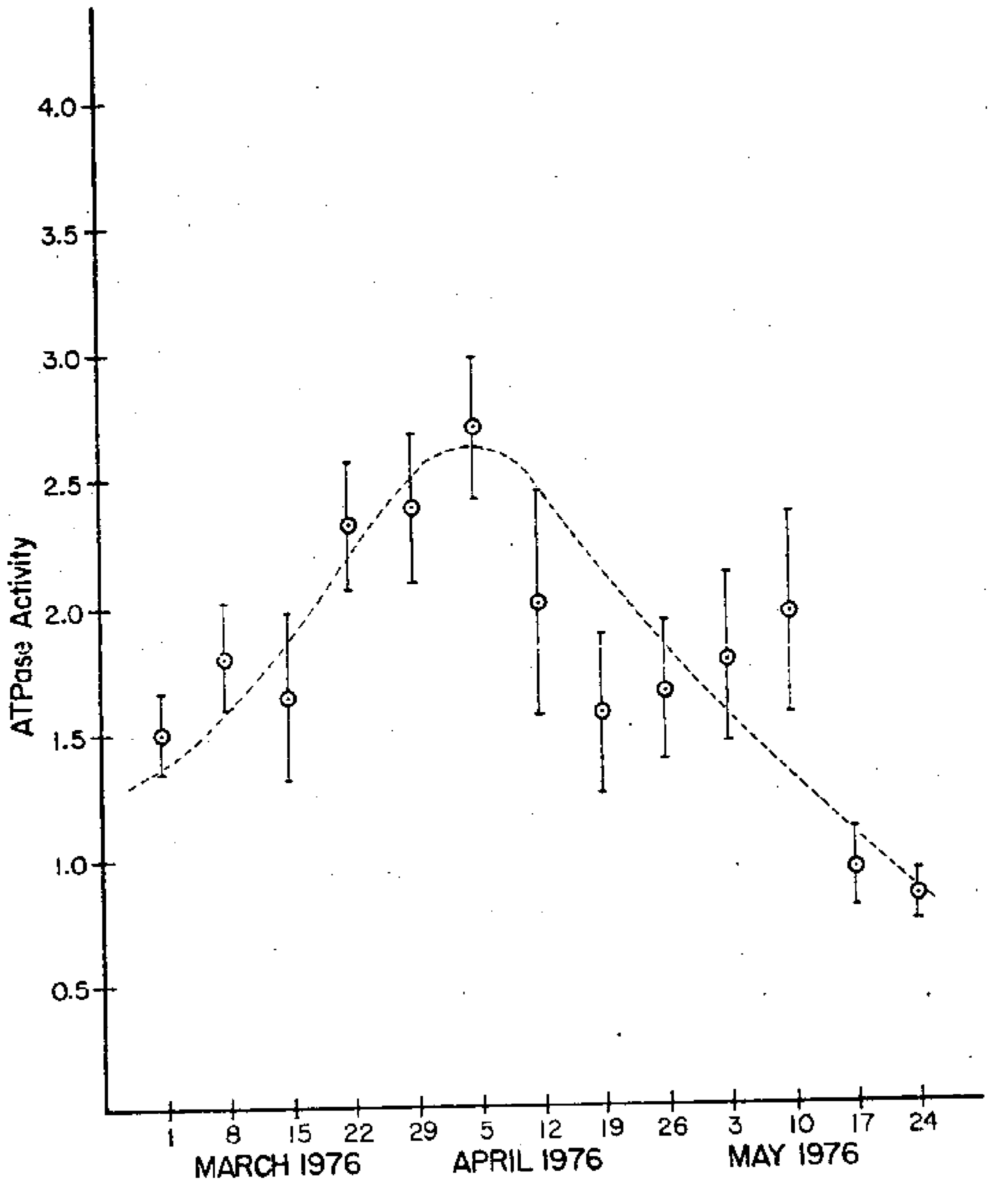

Figure 5. Gill Na,K, ATPase activity in Mad River strain yearlings. Each point is the mean ± S.E. of individual determinations on 6 fish.

Trinity Hatchery 2-year-olds

Figure 11, appendix, illustrates the extremely variable gill ATPase activity in Trinity Hatchery 2-year-olds. Although some values were high, many were very low. Some 2-year-old males were sexually mature, and since results of previous work (Zaugg and McLain, 1972) indicate smolting does not occur in those individuals, sexually mature males may account for the frequency of very low values in that group. Two-year-olds captured at Weitchpec subsequent to their release at the hatchery showed markedly higher values, as would be expected in a sample of migrating fish.

Washougal strain yearlings

Washougal strain yearlings from both hatcheries showed no clear peak through the season and averaged somewhat lower in gill ATPase than did the other yearlings at the respective hatcheries (fig. 12 and 13, appendix). During the peak of the Mad River strain smolt, March 22 through April 12, differences between Washougal and Mad River strain mean ATPase activities were statistically significant at the 1% level (March 22) and 5% level (March 29 and April 12) by the one-way analysis of variance test. Differences between Trinity Hatchery and Washougal yearlings, on the other hand, were not significant.

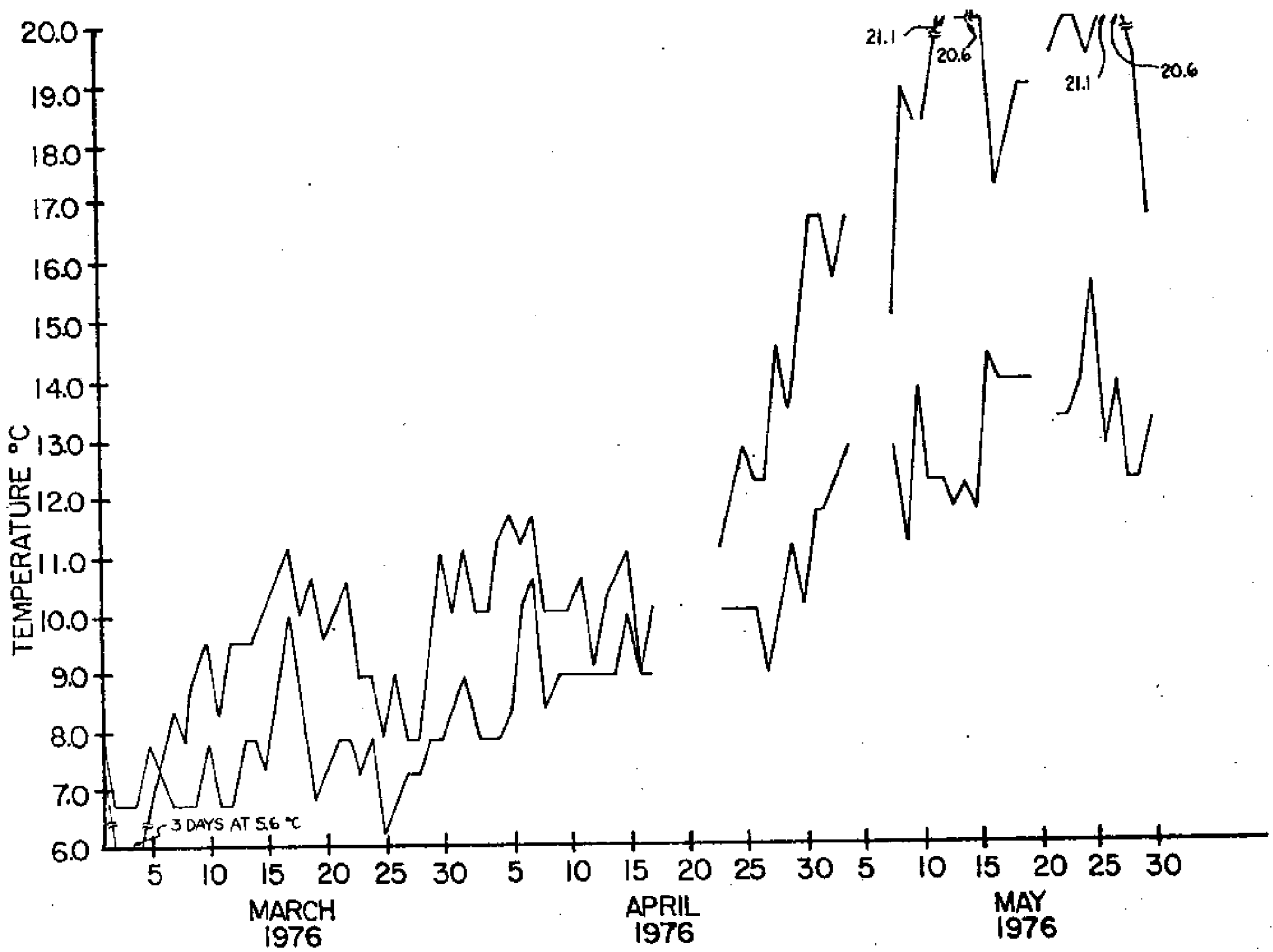

Figure 6. Daily high and low water temperatures at Mad River Hatchery from March 1 to May 30, 1976.

DISCUSSION

The metamorphosis of juvenile salmonids from the fresh water (parr) phase to the sea water preparatory (smolt) phase has been well documented and thoroughly described. Among the changes associated with smolting are the development of a silvery color, a decrease in the ratio of body weight to length (condition coefficient), and the appearance of migratory behavior. The validity of increased gill Na,K, ATPase levels as another index of smolting is supported by several investigations which have shown strong correlations between high ATPase levels and the smolt characteristics listed above. Zaugg and McLain (1970, 1972) pointed out that condition coefficient decreases as gill ATPase levels rise, and that the silvery color also coincides with high ATPase. (It is worthwhile noting, however, that we have measured low ATPase in fish which had both the silvery color and a low condition coefficient). More importantly, Zaugg and Wagner (1973) showed a correlation between high gill ATPase levels and migratory behavior. This is particularly relevant to steelhead hatchery management in view of the possible use of gill Na,K, ATPase values to indicate migratory readiness.

But elevated gill ATPase is a transitory phenomenon, as are the other smolt characteristics (Zaugg and McLain, 1970, 1972; Adams *et al.*, 1973, 1976; Hoar, 1976). Enzyme levels typically increase to a peak where they may remain for a time, and then decrease to parr levels if the fish does not move into a saline environment. The entire process is inversely related to water temperature--both the duration of smolting and the absolute values of the ATPase decline with increasing water temperature (Adams et al, 1976). The transitory nature of smolting means that an intermediate value for gill Na,K, ATPase would not by itself differentiate a fish coming into smolt condition from one reverting to parr status. If a population of juvenile steelhead is smolting synchronously and is sampled for ATPase activity at regular intervals through the smolting season, it would be relatively simple to identify intermediate enzyme values as representing either the smolting or desmolting (parr reversion) phases of the cycle. But in an asynchronous population this would be more difficult, especially if smolting were staggered in the population through an extended time period. Furthermore, gill ATPase values in such a population would be highly variable if random samples were chosen. Figure 7a represents gill ATPase activity in a hypothetical group of 7 fish which are smolting and regressing at different intervals in a 13 week period. Figure 7b represents a plot of the values which would result if gill ATPase in such a population were determined weekly. For example, at week 6, 3 fish are smolting and

2 are regressing, but figure 7b alone does not give that information.

In a general way, this is the type of pattern which the two hatcheries apparently produced (fig. 9 and 10, appendix). The Mad River yearlings showed a definite peak in early April, and the absence of low values (<1.5) for 3 weeks in late March and early April further identifies this period as the peak of smolting. A more correct estimate for the time at which most of the population was fully smolted might, however, be March 29, since low ATPase values did not appear for 2 weeks preceding or following that date. The pattern among Trinity strain yearlings at the Trinity Hatchery (fig. 3 and fig. 9, appendix) is more difficult to interpret for 3 reasons. First, there is no clear peak; second we recorded only 2 values of 3.0 or higher, compared to 9 at Mad River and 16 in the wild population; and third, low ATPase values were measured in every weekly sample except the first and fifth. The pattern suggests an extreme example of the model shown in fig. 7. The onset of smolting was apparently highly variable in the population, and in April a significant proportion of the population may have already been reverting to the parr condition. Two possible interpretations are, 1) that mean ATPase levels peaked about April 1, with the March 4 data representing an improbably high sample, or 2) that ATPase peaked on

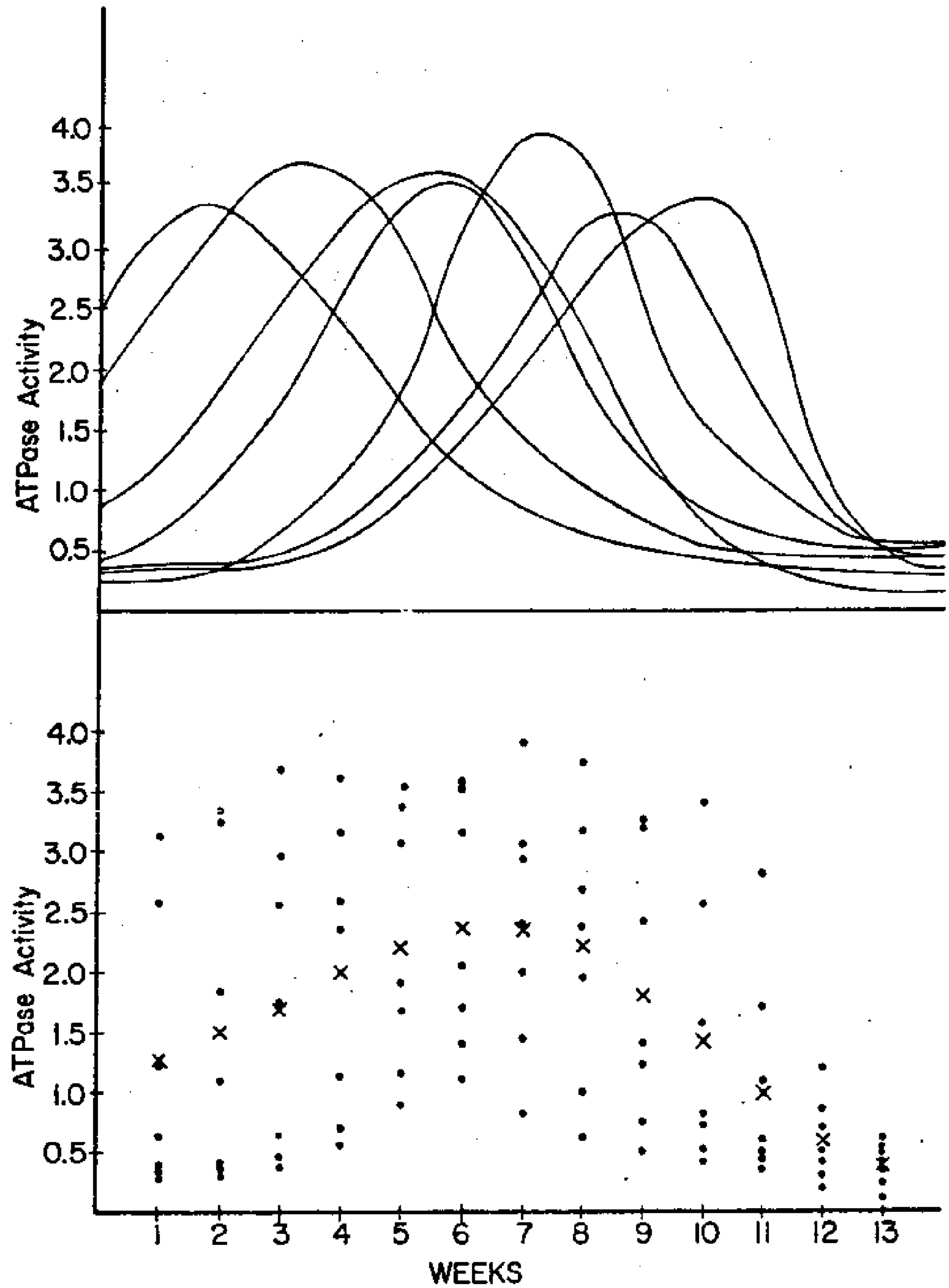

Figure 7(a). Model showing gill Na,K, ATPase elevation and decline in a hypothetical population of 7 fish smolting asynchronously.

Figure 7(b). Plot of ATPase activity which would result if enzyme levels in the population represented in Figure 7(a) were determined weekly.

March 4 or before. By late April increasing water temperatures (fig. 4) brought on a complete reversion to parr condition in the hatchery.

As pointed out earlier, gill ATPase values in wild Trinity River steelhead do not represent a random sample of the river population. Nevertheless the increase and decline of ATPase, together with the numbers of migrating smolts estimated from the catch in nets at Weitchpec (Table 1), probably give a valid picture of the smolting pattern in the river. Clearly the smolting peak in the wild population was at least a month later than at Mad River Hatchery and perhaps as much as 2 months later than at the Trinity Hatchery. The fact that the apparent peak of migration was some 2 to 3 weeks later than the peak in gill ATPase is consistent with the general picture of smolting reported elsewhere. Conte and Wagner (1965) reported that morphological smolt characteristics, as well as ability to survive in sea water, preceded the appearance of migratory behavior by several weeks.

The reasons for the difference in smolting patterns among the 3 populations are unclear. Wagner (1974a) did an extensive investigation of factors which influenced the onset and duration of smolting in steelhead trout, and he concluded that increasing day length was the major environmental cue. Temperature was an important modifier--low temperatures extended the season and high temperatures shortened it. But Wagner also gave evidence that smolting is part of an endogenous cycle since fish reared in constant darkness in his study also showed signs of smolting. He stated further that, "Factors responsible for transformation apparently reside entirely within the animal and become functional in some fish when they reach a certain size (physiological age) even in the absence of light and temperature changes."

Both hatcheries have artificial light incident on the raceways throughout the hours of darkness. Light intensities, however, are low--a maximum of 10 lux 5 cm above the water surface was measured at Mad River Hatchery. Light intensity was not measured at the Trinity Hatchery, but it is much lower than at Mad River. Since the smolting pattern at Mad River Hatchery was more nearly normal (as gauged by the Trinity River pattern), we tentatively conclude that altered photoperiod is not alone responsible for abnormal smolting.

Mean weekly water temperatures at the two hatcheries differed markedly in the year beginning March, 1975. Trinity Hatchery water which, as previously pointed out, originates in the deep, cold levels of Trinity Lake, was above 10° only from early July to early October, and only from late July to mid August did it rise above 13° (fig. 14, appendix). From the end of October to early March mean temperatures fluctuated between 6° and 8°. In contrast, Mad River weekly mean temperature reached 10° in late April, climbed steadily to highs exceeding 20° in late July and August, remained above 19° until mid September, and did not drop back to 10° until early November (fig. 15, appendix). Although Trinity River water temperatures often exceed 20° in the summer months below Lewiston Dam's zone of influence, many of the wild steelhead are in the tributaries through the warm season and consequently may not be subjected to temperatures that high. It is probably fair to say that wild Trinity River steelhead experience a seasonal temperature variation similar to that at Mad River Hatchery, but with cooler temperatures lasting later in the spring and appearing earlier in the fall, and with colder water, down to 2° at times, during the winter months.

The major differences in the annual temperature cycles between the three study environments appear to lie in the absence of high summer and early fall temperatures in the Trinity Hatchery. Winter temperatures are comparable to those at Mad River Hatchery and 2° to 4° warmer than in the Trinity River. It is tempting to speculate that a natural temperature regime contributes to the synchronous onset of smolting in a population, and that the somewhat abnormal temperatures at the Trinity Hatchery were at least partly responsible for both asynchronous smolting and the generally reduced levels of gill ATPase in the population. Indeed, Wagner (1974a) concluded that photoperiod and temperature reinforce each other, and that the maximal smolting response occurs when the two are in phase.

Regardless of whether or not the seasonal water temperature differences were responsible for differences in the onset of smolting, it seems clear that high water temperatures hastened the end of smolting in both hatcheries. Mean ATPase values of Trinity Hatchery yearlings dropped sharply on May 6; mean water temperatures reached 14° on May 2, 15° on May 5, and continued high[1] thereafter (fig. 4). At Mad River Hatchery, mean daily temperatures first exceeded 15° on May 10, and 1 week later ATPase values had dropped to a mean of less than 1.0. In the Trinity River, mean daily temperatures (fig.2) fluctuated around 15° from May 10 to June 12, when they abruptly approached 17°; the number of wild steelhead (migrants) captured in the nets dropped from 144 in the week ending June 9, to 13 in the week ending June 15. At first glance, it would seem that smolting in the wild population was

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[1]We should point out that high water temperatures in the spring at Trinity Hatchery are uncommon. Precipitation in the watershed in 1975-76 was far below normal; as a consequence only minimal amounts of water were passed through Lewiston Reservoir, allowing reservoir water to become atypically warm as the season progressed.

compatible with 15° temperatures, and that only after an additional 2° rise did smolting end. But temperatures experienced by wild smolts in the one or two weeks preceding their capture are not necessarily represented by water temperatures at Weitchpec. Upstream sections of the river are somewhat cooler because of the influence of colder tributaries and, in fact, some of the outmigrants may have been in tributaries as recently as one or two days before their capture. Furthermore, temperature stratification in the deep, slow moving sections has been observed (Hubbell, pers. comm.) and could unquestionably provide a cooler environment for resident fish. Whether the end of migration was the result of higher water temperatures or simply the end of the normal smolting season is impossible to tell, but the work of Adams et al. (1973, 1976) points to the former choice.

A third variable among the populations was diet. The hatchery steelhead were fed Oregon Moist Pellet at a rate calculated to bring most to a length of 15 cm or greater at 1 year of age. Some yearlings from both hatcheries had attained lengths greater than 22 cm when the study began in early March. Lengths in excess of 23 cm were noted occasionally as the season progressed. On the other hand, preliminary scale analyses of 59 wild Trinity River smolts indicated that only one yearling exceeded 18 cm in length. It is reasonable to assume that reduced feeding during the colder months is an important factor in the slower growth of wild fish. Given these differences in feeding patterns, one might speculate that earlier smolting in hatchery fish was brought on because sustained feeding throughout the colder periods allowed growth and development to continue, while at the same time wild fish were eating very little. We have seen no published reports which directly support this hypothesis, but Wagner (1974a) reported that (some) steelhead kept in constant darkness smolted when they reached sizes between 19 and 21 cm, even in the absence of environmental cues.

Results of California Department of Fish and Game netting operations at Weitchpec give some credence to the idea that rapid growth may be primarily responsible for early smolting. Approximately 98,600 Trinity strain yearlings, with a mean fork length of 19.9 cm, were released in late April and early May, and 461 (0.47%) were subsequently captured in the nets. In contrast, of approximately 114,900 Klamath River yearlings (mean fork length 16.4 cm) released by the Trinity Hatchery in the same time period, 841 (0.75%) were captured at Weitchpec[1]. Although genetic differences must be considered, the smaller mean length of the Klamath fish appears to correlate with greater downstream movement. Furthermore, 59% of the Trinity strain yearlings captured

[1]Preliminary data from William Heubach, California Department of Fish & Game.

in the Weitchpec nets were taken before May 15, while only 0.7% of the Klamath yearlings captured had been taken by that date. The bulk of the latter group (77%) were taken between May 25 and June 7[1]. These results clearly indicate that the smaller Klamath yearlings were migrating later in the season and the results further suggest that significant numbers of Trinity yearlings may have reverted to parr status by the time of their release and consequently failed to migrate. We must again urge caution in the interpretation of this data because of the unknown effects of genetic differences between the two races.

Even within the Trinity stock, genetic variability may further complicate the picture. The California Department of Fish and Game has in the past introduced steelhead from other sources into the Trinity River. It is impossible to tell to what extent these introductions may have changed the gene pool, what effect this might have on smolting, and whether both wild and hatchery populations would be equally affected.

Gill ATPase levels in Trinity Hatchery 2-year-olds (fig. 11, appendix) averaged lower than levels in Trinity yearlings until the first week in April, after which mean values were generally the same. More significantly, the 2-year-olds had a much higher percentage of very low (<.5) values than did the yearlings through April 29--

[1]Preliminary data from William Heubach, California Department of Fish & Game.

30% vs. 4%. This is consistent with observations made by Zaugg and McLain (1972), who concluded that many hatchery-reared 2-year-old steelhead, including all sexually mature males, did not smolt. But some 2-year-olds released at the hatchery did migrate, as evidenced by the subsequent capture of 141 at Weitchpec (Heubach[1], pers. comm.), and ATPase levels in those fish were generally high (fig. 11, appendix).

Washougal strain yearlings from both hatcheries showed no discernible trends in gill ATPase activity during the course of the study (figs. 12 and 13, appendix). The only conclusion that can be drawn, considering the small (3) weekly sample sizes, is that neither population smolted synchronously during the study period. But the low-intermediate values which seemed to predominate in the samples, plus 2 relatively high values from the Mad River Hatchery, indicate to us that at least some smolting was occurring. It is also interesting that 1.06% of the Washougal strain yearlings released at the Trinity Hatchery (mean fork length 17.7 cm) were captured at Weitchpec, vs. 0.47% of the Trinity strain yearlings (mean fork length 19.9 cm) (Heubach[1], pers. comm.).

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[1]William Heubach, Anadromous Fisheries Branch, California Department of Fish and Game.

CONCLUSIONS

The onset of smolting of steelhead yearlings in both the Trinity and Mad River Hatcheries occurred several weeks prior to the smolting of wild steelhead in the Trinity River. Trinity Hatchery yearlings showed no clear peak in gill Na,K, ATPase activity; the data indicates the population was smolting asynchronously, the onset occurring before the study was begun on March 4. Mad River Yearling mean ATPase levels peaked in early April, but that group also showed some evidence of asynchronous smolting. Mean gill ATPase levels in wild Trinity River steelhead increased steadily to a peak on May 11, then declined steadily until June 15.

The reasons for the differences in smolting patterns in the three locations are unclear. Artificial lighting of raceways at night is tentatively ruled out because of the extremely low light levels at the water surfaces. Seasonal differences in mean water temperatures between the 3 locations may have been a factor, especially in the asynchronous pattern at the Trinity Hatchery. Sustained feeding at the hatcheries during the colder months should be seriously considered as a possible reason for early smolting.

The abrupt end of smolting in both hatcheries coincided with the appearnce of water temperatures in the range of 14°C to 18°C. In the Trinity River, gill

ATPase values from wild steelhead captured at Weitchpec remained relatively high until the end of the study (June 15), but a sharp decline in the numbers of migrating fish in mid June coincided with the appearance of mean temperatures approaching 17°C and indicated that smolting had stopped.

ACKNOWLEDGMENTS

Several people aided us greatly in the development and completion of this project. Paul Hubbell, Anadromous Fisheries Branch, California Department of Fish & Game, recognized the need for a study such as this, worked with us in the planning stages and consulted with us regularly during the course of the work. William Heubach, also of California DFG, continually gave us invaluable assistance, and hatchery managers Gerald Bedell (Trinity) and Robert Will (Mad River) kindly provided unlimited use of their facilities.

We would also like to thank Dr. Harry Wagner, Research Supervisor, Oregon Department of Fish and Wildlife, for his interest in the project and his careful review of the manuscript. This work was supported by Grant No. 04-6-158-44028 to Humboldt State University from the National Sea Grant Program, NOAA, U. S. Department of Commerce.

Notwithstanding the assistance of the people and agencies named above, the authors take full responsibility for any errors in fact or judgment in this report.

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APPENDIX

Figures 8 through 15

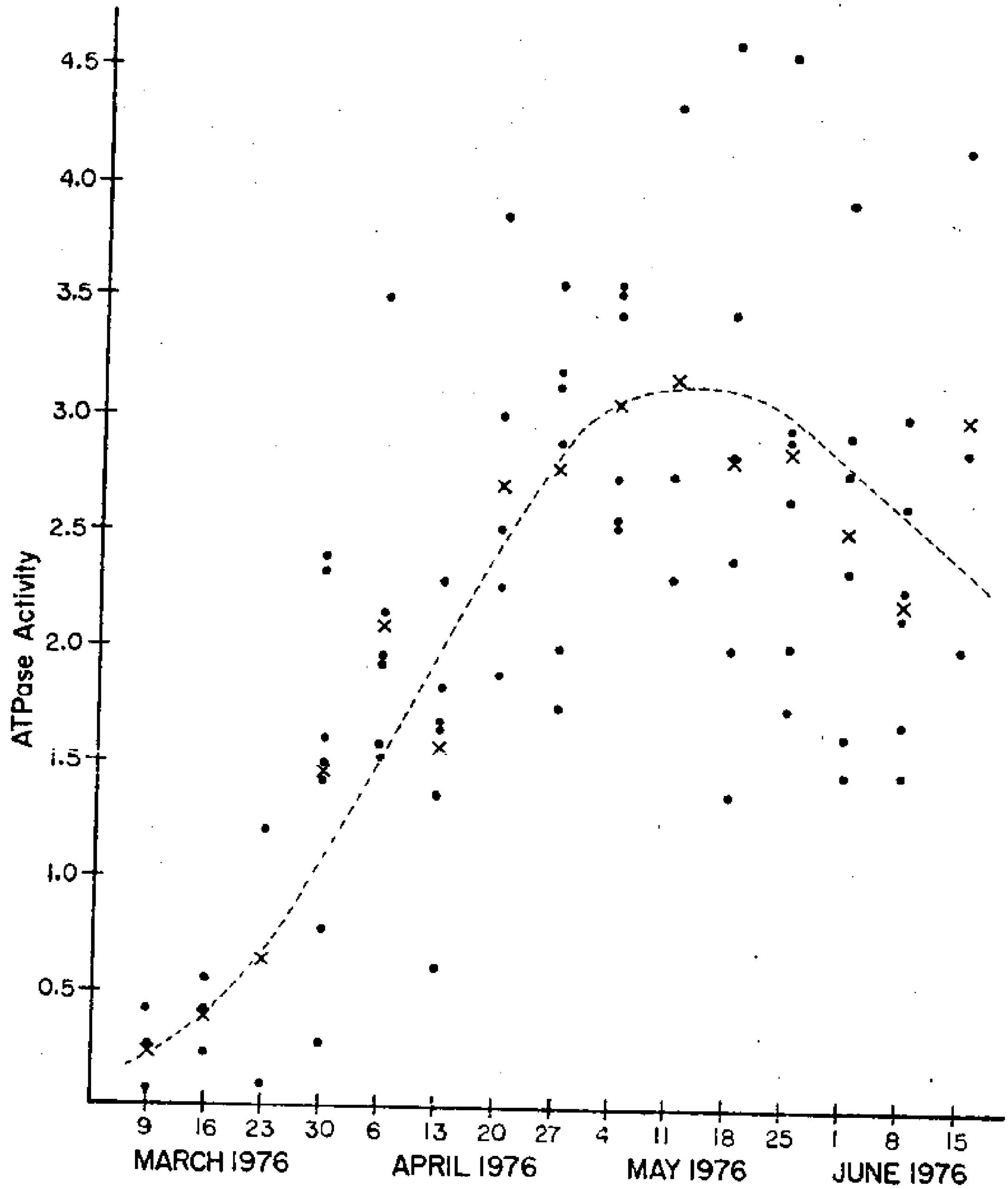

Figure 8. Individual gill ATPase determinations of wild steelhead captured at Big Bar (March 9 - 23) and Weitchpec (March 30 - June 15).

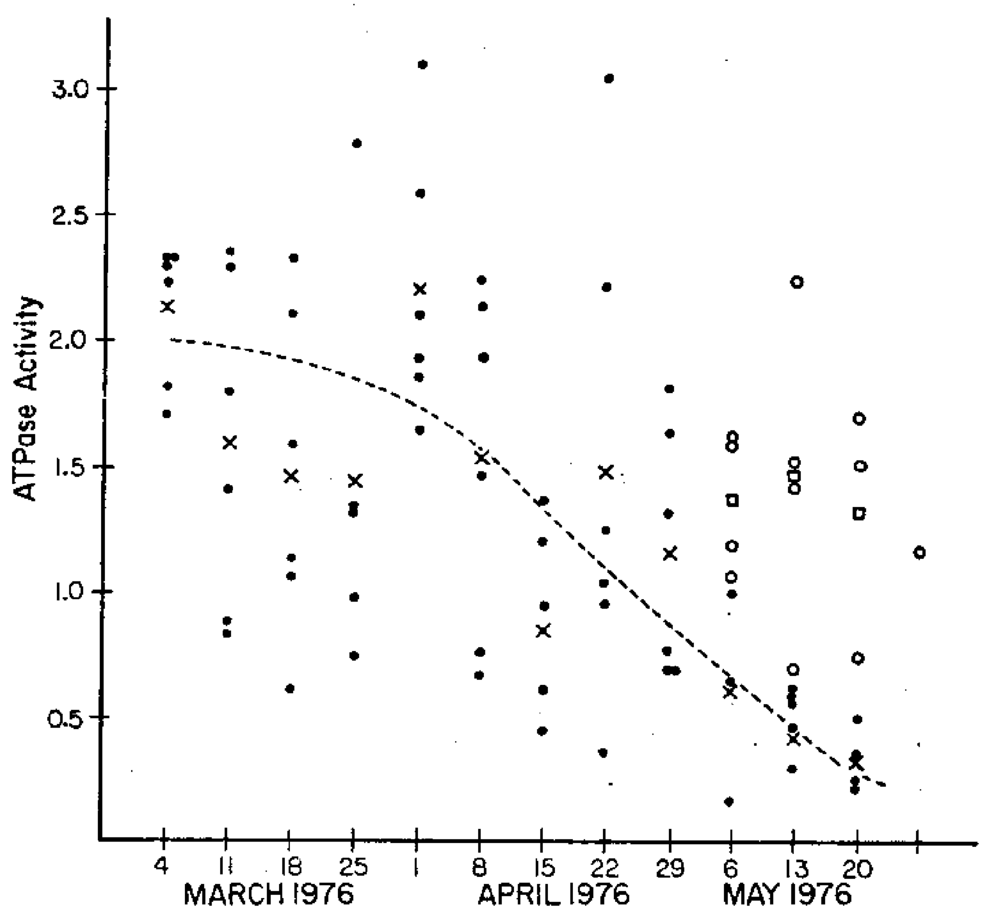

Figure 9. Individual gill ATPase determinations of Trinity strain yearlings sampled at the hatchery (●) and at Big Bar (o). Symbols X and ◘ are means.

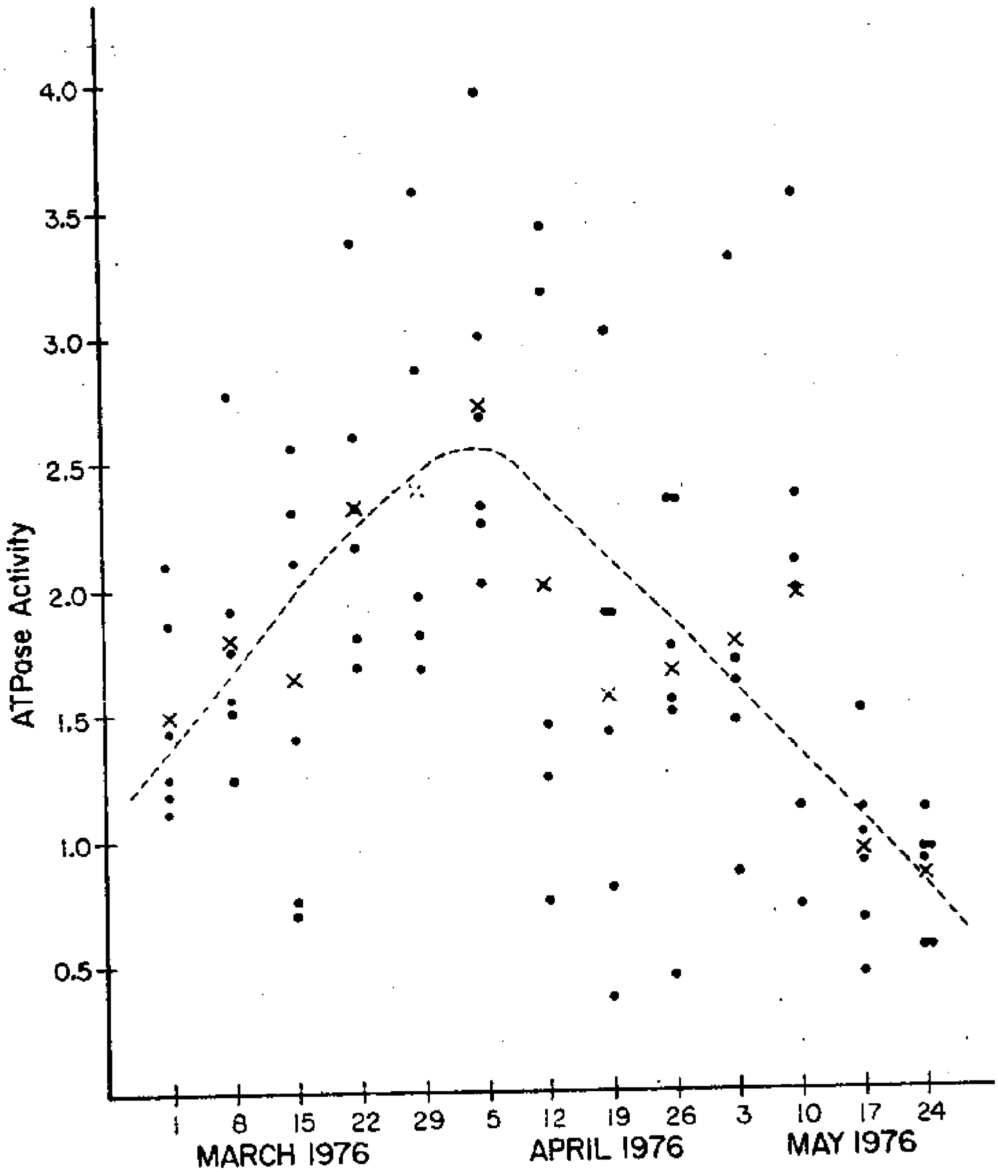

Figure 10. Individual gill ATPase determinations of Mad River yearlings.

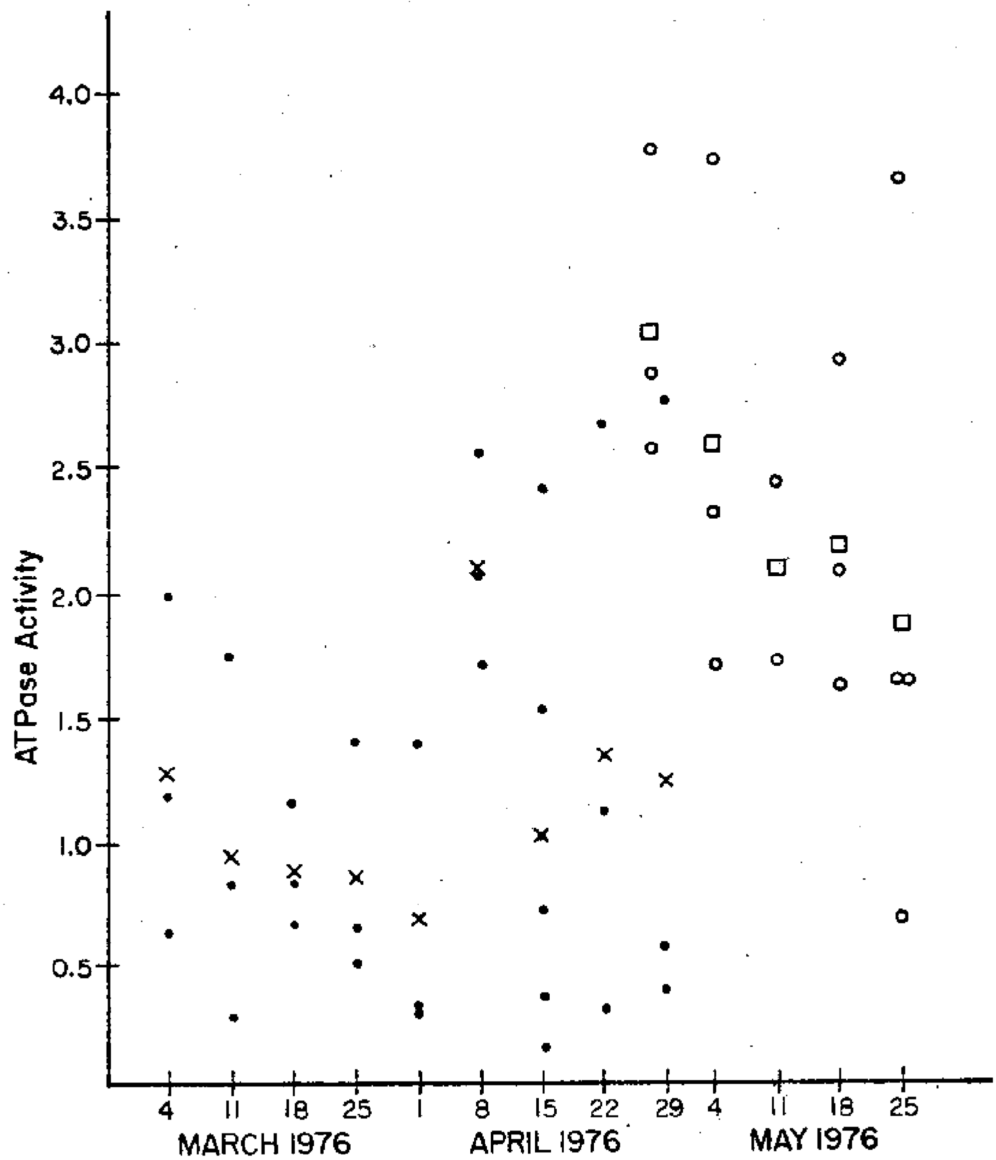

Figure 11. Individual gill ATPase determinations of Trinity strain 2-year-olds sampled at the hatchery (●) and at Weitchpec (o) subsequent to their release. Symbols X and ◻ are means.

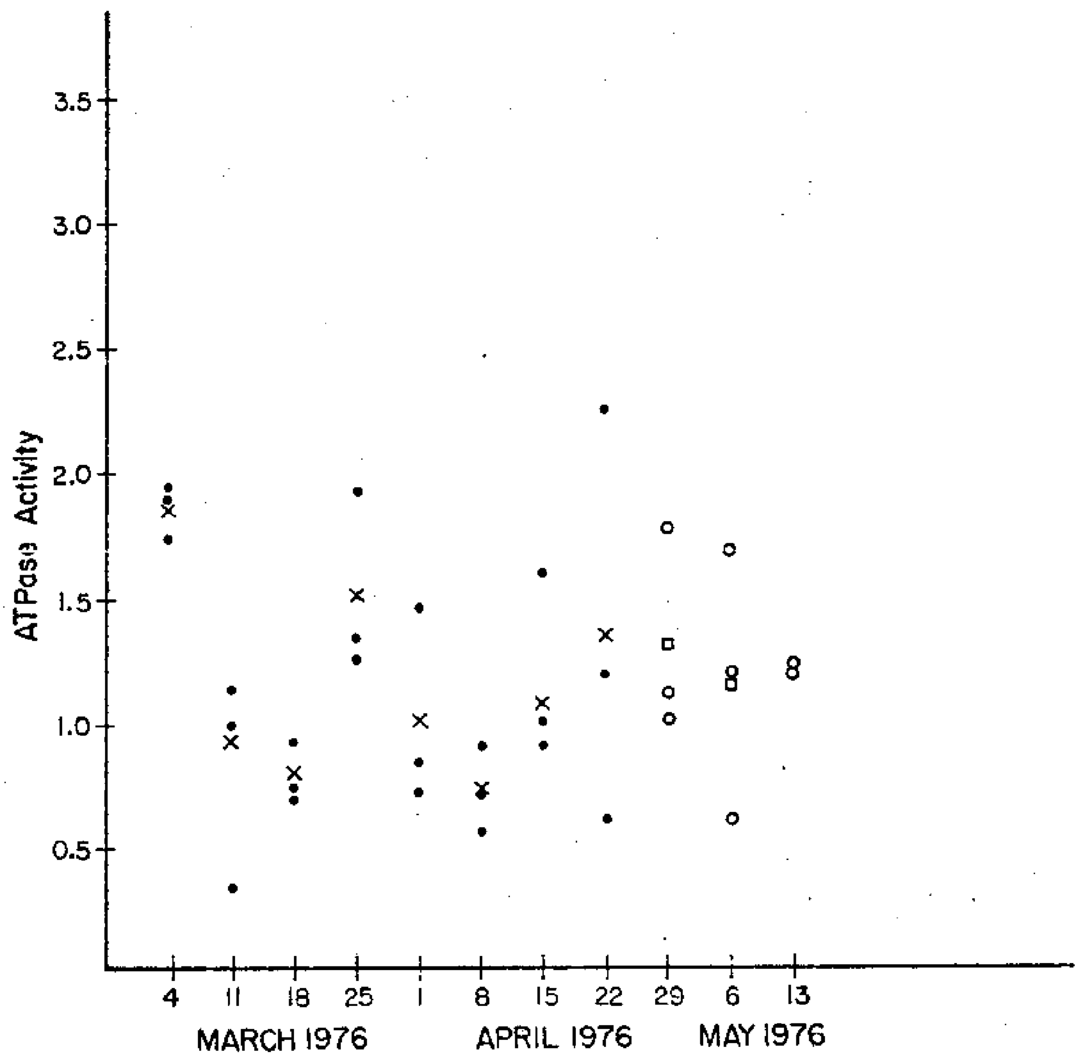

Figure 12. Individual gill ATPase determinations of Washougal strain yearlings sampled at Trinity Hatchery (●) and from the Trinity River at Big Bar (o). Symbols X and □ are means.

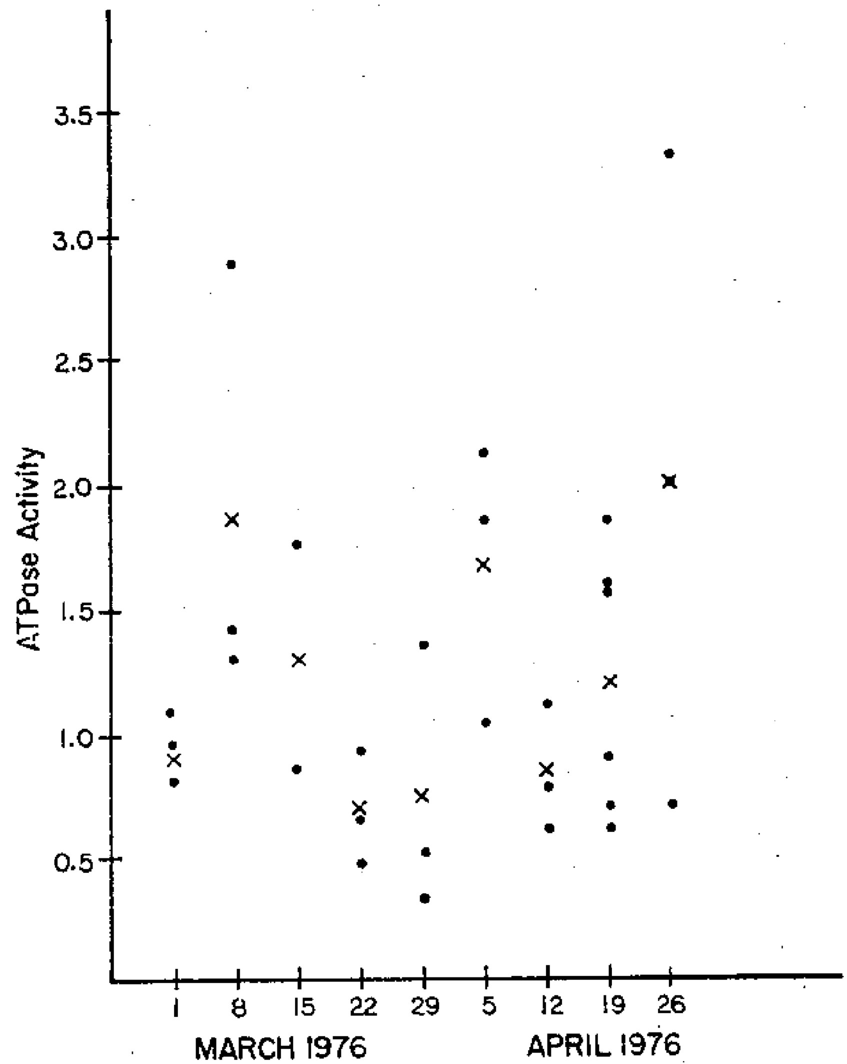

Figure 13. Individual gill ATPase determinations of Washougal strain yearlings at Mad River Hatchery. X represents mean.

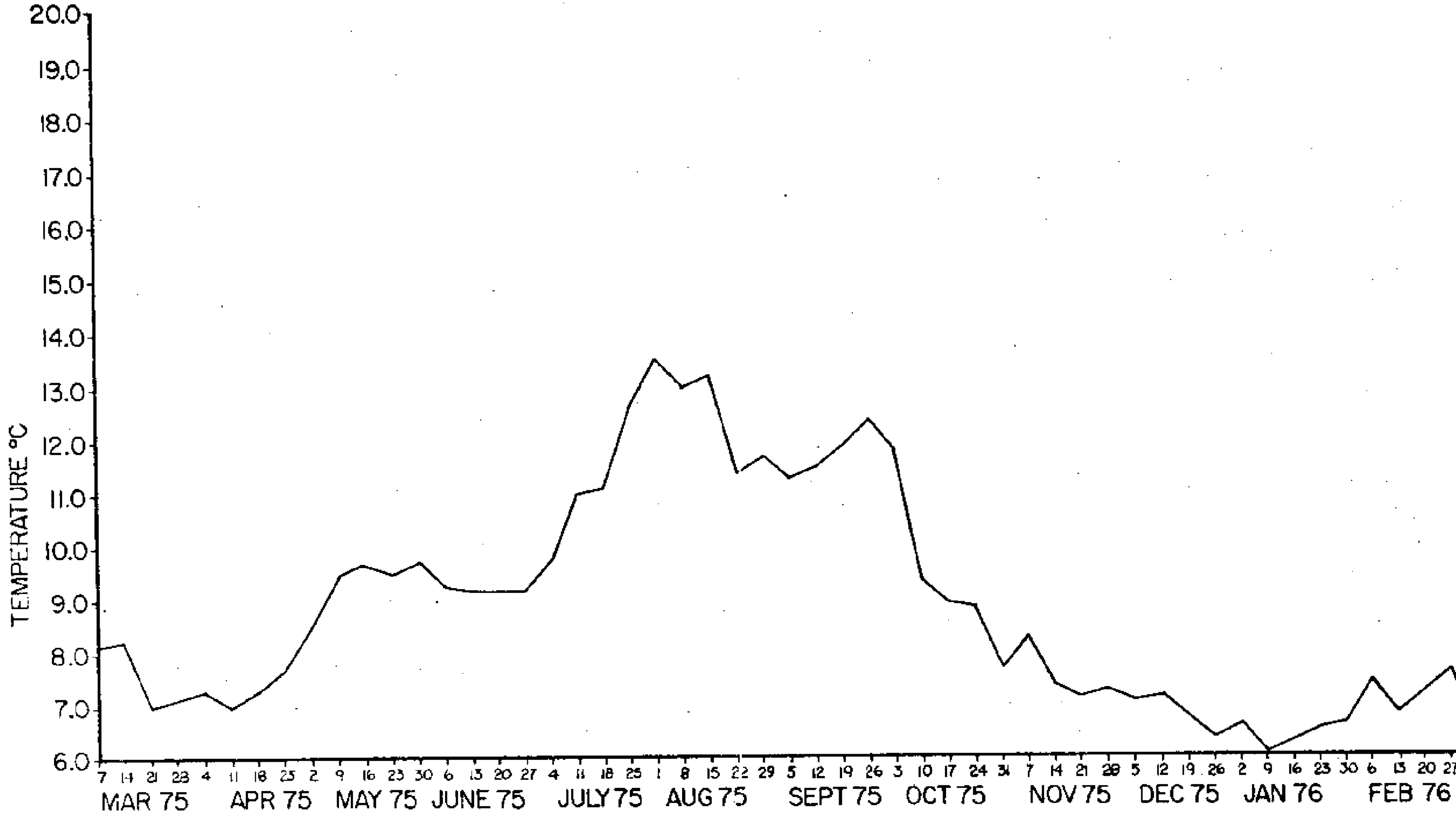

Figure 14. Weekly mean temperature of Trinity Hatchery water, March 7, 1975, to Feb. 29, 1976. Daily means were used to calculate weekly means.

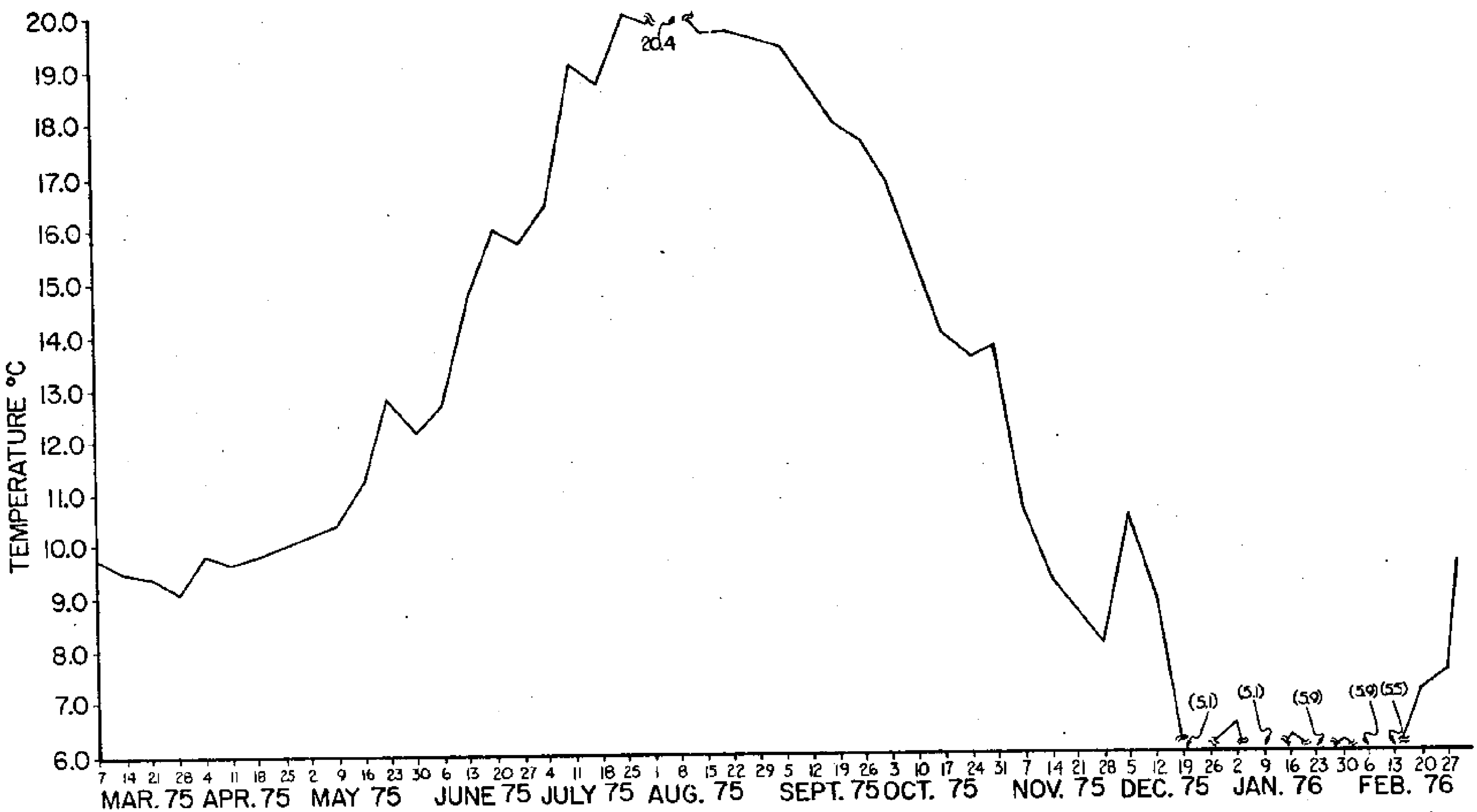

Figure 15. Weekly mean temperature of Mad River Hatchery water, March 7, 1975 to Feb. 29, 1976.