The Use of Electromyogram Telemetry to Estimate Energy Expenditure of Adult Fall Chinook Salmon

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Summary

Excess energy expenditure during the upstream migration of adult fall chinook salmon (*Oncorhynchus tshawytscha*) may reduce spawning success or lead to increased pre-spawning mortality. Recent advances in biotelemetry now make it possible to assess how the energy budget of an adult salmon would be spent during upstream migration through the Columbia River hydroelectric system. The objective of this study was to evaluate the use of physiological telemetry to estimate the energy expended by fall chinook salmon at different swimming velocities. An electromyogram (EMG) telemetry system was used to obtain, transmit, and record the EMGs produced during muscle activity. The EMG telemetry system provides a means to evaluate the effects of structural or operational changes in the hydropower system on energy expenditure and reproductive success of upstream migrant adult salmon. Seven adult salmon (71.5 to 106 cm FL) were tagged and exercised in a respirometer over a range of water velocities at 15º C and 20º C. There was no difference in oxygen consumption between individual fish ($P = 0.671$), temperatures ($P = 0.391$), or size classes ($P = 0.535$). The EMG pulse rates and oxygen consumption by test fish were positively correlated with swimming speed. Also, oxygen consumption was positively correlated with EMG pulse rate, and was within the range observed in other EMG studies of adult salmon. The average EMG pulse rate of small (≤ 90 cm FL) fall chinook salmon was significantly faster than that of large (> 90 cm FL) fall chinook salmon ($P = 0.003$), and the EMG pulse rate increased as the swimming velocity increased for both size classes. Comparisons of energy expended (based on oxygen consumption) versus energy available (based on literature values) suggested that adult fall chinook salmon that are delayed longer than 5 days per hydroelectric dam may have insufficient energy reserves to complete spawning. Results of this study suggest that further investigation of the energy expended by adult chinook salmon during the upstream migration is warranted.

Acknowledgments

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1.0 Introduction

Background

Most anadromous salmonids do not feed during the spawning migration phase of their life-cycle (Raleigh et al. 1986). Therefore, the energy budget a fish has at the beginning of its journey is fixed and must be partitioned among basic metabolism, active metabolism, and tissue growth. How the energy budget of a fish is allocated depends on its life history (Adams and Breck 1990), but during the spawning migration phase of anadromous salmonids, energy is partitioned relative to effort required to swim upstream (Idler and Clemens 1959; Brett 1965, 1995; Hinch et al. 1996).

Natural barriers that affect fish migration include distance traveled, strong currents, rapids, waterfalls, and gravel bars (Brett 1965). Artificial structures such as hydroelectric dams also affect fish passage. The physical characteristics created by these dams and the ability of fish to find fishway entrances influence the amount of time fish spend in the tailrace (reviewed in Dauble and Mueller 1993). Changes in flow regimes at dams also affects salmonid migration rates, passage success, and fallback behavior (Bjornn and Peery 1992). Migration delays at hydroelectric dams in the Columbia River Basin range from a few hours to several days per dam (Dauble and Mueller 1993; Bjornn et al. 1994; Mendel et al. 1992, 1994). The time spent migrating through the dam and reservoir system is of concern because a lengthened migration period could deplete the fish's energy reserves, resulting in reduced spawning success (Berman and Quinn 1991) or increased pre-spawning mortality (Beiningen and Ebel 1970; Gray 1990; Snelling et al. 1992). Loss of production potential for returning adults is a particular concern for Snake River salmon stocks that are listed under the Endangered Species Act (ESA).

Humans have the ability to mitigate some challenges salmon face during their upstream migrations through the Columbia River system hydropower complex. For example, several proposals to aid in recovery of ESA-listed fish focus on reducing passage time at hydroelectric projects (NWPPC 1994; NMFS 1995). These proposals include increasing adult attraction flows, installing and/or redesigning fish ladders, reducing water temperature within adult fishways, and implementing temperature control measures, via reservoir releases, in the lower Snake River. Determining the effectiveness of these management recommendations will require further monitoring and evaluation. Recommended studies also include determining the impacts of migration duration on reproductive success and pre-spawning mortality. Studies relating to hydropower operation and migration behavior are needed because the energy requirements of salmon during their upstream migration are not currently available (Dauble and Mueller 1993). Such data would provide a means for evaluating the physiological response of adult fish to each of the management recommendations (Brett 1995).

Physiological telemetry now makes it possible to assess how the energy budget of an adult salmon would be spent in response to structural or operational changes in the hydroelectric system. A number of methods have been used to determine physiological telemetry correlates of oxygen consumption (i.e., fish activity), including the transmission of telemetry signals for heart rate (Priede

and Young 1977; Lucas et al. 1991), tailbeat frequency (Stasko and Horrall 1976; Ross et al. 1981), respiration rate (Oswald 1978; Rogers and Weatherley 1983), and locomotor muscle electromyograms (Rogers et al. 1984; McKinley and Power 1992; Hinch et al. 1996). Each of these methods is capable of providing an accounting of activity for free-ranging fish and a measure of metabolic cost; the use of these techniques for monitoring fish populations is reviewed in Lucas et al. (1993).

Objective and Scope

The long-term objective of this study was to estimate the absolute energy expenditure of adult fall chinook salmon (*Oncorhynchus tshawytscha*) ascending the Columbia River to spawn. We conducted laboratory respirometry experiments to evaluate the use of electromyogram (EMG) radio transmitters as a means to examine the relationship between EMG values and oxygen consumption in adult fall chinook salmon. Tests were performed over a range of swimming speeds at two temperatures. Normally the second phase of a study like this would include a field investigation where the oxygen - EMG relationships determined from the laboratory would be used to develop an energetic index for free-living fish (e.g., Hinch et al. 1996; Demers et al. 1996). Funding constraints prohibited us from initiating this field investigation, and hence, we were not able to estimate absolute energy expenditure of migrating adult fall chinook salmon. However, we used results from our laboratory respirometry experiments and values from the literature to develop a conceptual bioenergetics model for adult fall chinook salmon that spawn in the Hells Canyon Reach of the Snake River; this model is presented here.

2.0 Methods

Fish Collection and Handling

In September, 1995, we obtained a total of 19 adult fall chinook salmon (71.5 to 106 cm FL) from the Priest Rapids Salmon Hatchery on the Hanford Reach of the Columbia River near Priest Rapids Dam (Rkm 639) that had returned to the hatchery to spawn. Salmon were transported in an aerated tank from the hatchery to the Pacific Northwest National Laboratory located 80 km away in Richland, Washington. On arrival at our facility, fish were held at 17.4º C on well water in a covered rectangular (~3 m long, 1.3 m wide, and 1 m deep) raceway.

The day following collection, we conducted surgery on the fish to insert the EMG transmitters. EMG radio transmitters (Lotek Engineering, Aurora, Ontario, Canada) were 5 cm long, 1.5 cm in diameter, and weighed 20 g in air. They had two steel-wire electrodes and an antenna trailing from one end. The EMG radio transmitter is part of a biotelemetry system capable of obtaining, transmitting, and recording EMGs produced during muscle activity. The EMGs are records of bioelectric potential and are strongly correlated with the strength and duration of muscle contraction. As the activity level of an animal increases, the EMG pulse rate increases because the interval between muscle contractions decreases. Oxygen consumption is also strongly correlated with muscle contraction; oxygen consumption increases as activity increases. Therefore, there is a positive relationship between the consumption of oxygen and the EMG pulse rate. Because oxygen consumption is an indirect measure of active metabolism (Adams and Breck 1990; Cech 1990), the EMG signal becomes a measure of active metabolism. Additional details on the EMG technology are given in Kaseloo et al. (1992), Hinch et al. (1996), and Demers et al. (1996).

Before surgery, fish were anesthetized by immersion in MS-222 (Tricaine methaneosulfonate) at concentration of 1:10,000 to 1:20,000. Once a fish reached stage 4 anesthesia (Summerfelt and Smith 1990), it was placed ventral side up in a V-shaped surgical table. During surgery, gills were irrigated with fresh water or water containing MS-222 at the concentrations described above to maintain respiration at stage 4 anesthesia. To place the EMG transmitter, a 3-cm incision was made into the abdominal cavity just anterior to the pelvic girdle. A hollow spinal needle (25 cm long, 15 ga) containing a sharpened stylet was inserted in the incision and pushed through the mid-lateral musculature approximately 10 cm posterior to the pelvic fins. After removing the stylet, the antenna wire was threaded through the needle until it protruded from the far end. The hollow needle was removed by pushing it through the hole and over the extended antenna wire.

Once the antenna wire was in place, the electrodes were implanted in the red muscle tissue. As shown in Figure 1, each electrode was capped with a 14K gold barb designed to catch in the red muscle tissue and anchor the electrode firmly in place.

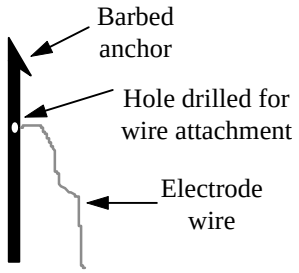


Figure 1. Electrode wire attached to a gold barb that anchored the electrode in the red muscle tissue.

Using the tool shown in Figure 2, the electrode anchor was inserted into the body cavity through the initial incision.

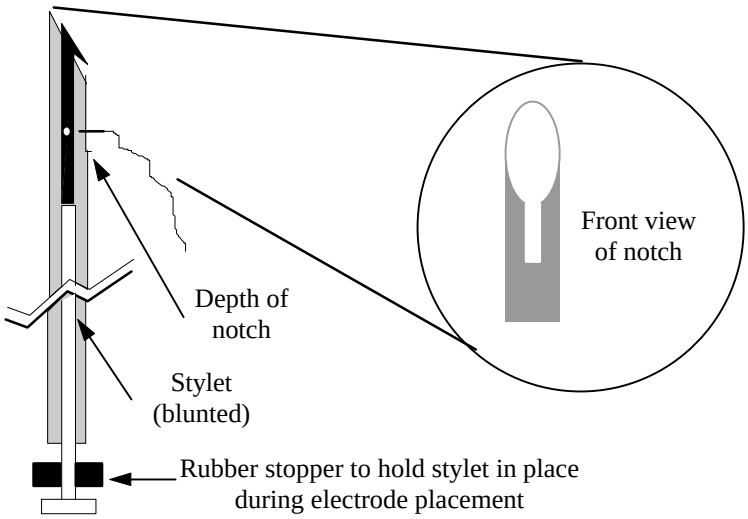


Figure 2**.** Tool used to facilitate electrode insertion into the red muscle of fish.

The tool entered the muscle (through the ribs) just posterior to the swim bladder and was pushed through the muscle at a 45 to 60 degree angle toward a point just behind the posterior edge of the dorsal fin, just above the lateral line and just under the skin. This location is the area of maximum red muscle thickness in fall chinook salmon. The anchor was discharged from the tip by plunging the stylet and pushing the anchor and electrode wire into place. The electrode wire was then tugged gently without moving the instrument. The radio receiver was turned on during the surgical procedure and set to scan for the frequency of the transmitter being emplaced. When done properly, the electrode anchor twisted and lodged under the skin exactly where it was discharged and there was a definite reduction in the pulse rate of the transmitter. The second electrode was placed approximately 5 mm posterior to the first in the same manner (Figure 3).

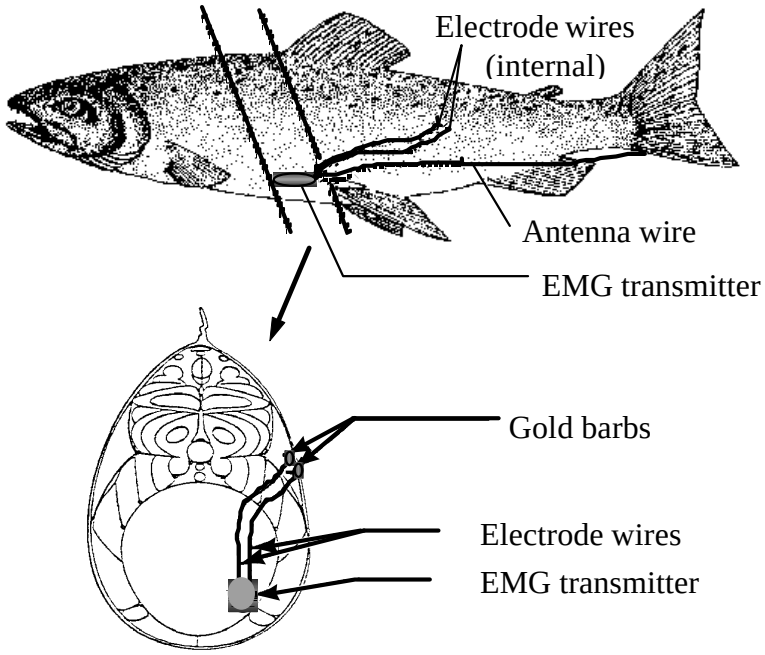


Figure 3. Electrode placement in the fish (modified with permission from McKinley et al. 1994).

The transmitter was then inserted into the body cavity and the incision closed with four or five monofilament nylon sutures placed 0.6 cm apart. Average time for surgery was 10.7 minutes.

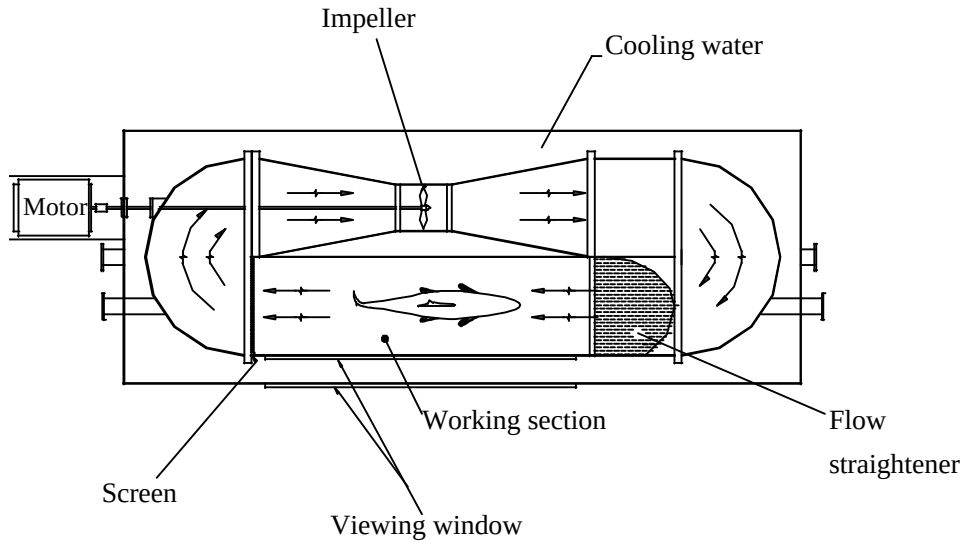
Following the last suture placement, a lavage needle was used to inject about 1 cc/4.5 kg fish of the antibiotic Oxybiotic-100. The incision was swabbed with a concentrated providone iodine solution of full strength Betadine and then smeared with a triple antibiotic ointment, Zinc-Neomycin Sulfate-Polymyxin B Sulfate Ointment, USP. The antenna exit wound also was treated in this manner. A numbered disk tag was placed in the dorsal musculature for identification and the fish was held in a 1.8-m circular tank until it revived. All fish recovered completely within 30 minutes of surgery.

After surgery fish were kept in a 6 m outdoor circular pond supplied with well water. To shade the fish and prevent escape, half the pond was covered with a tarp and the other half with netting (mesh size 2.5 cm). Fish were treated daily with a static bath of formalin (37% formaldehyde) at a concentration of 0.167 ml/L (1:6000). Fish were allowed to recover from surgery for two weeks before being exercised in the respirometer.

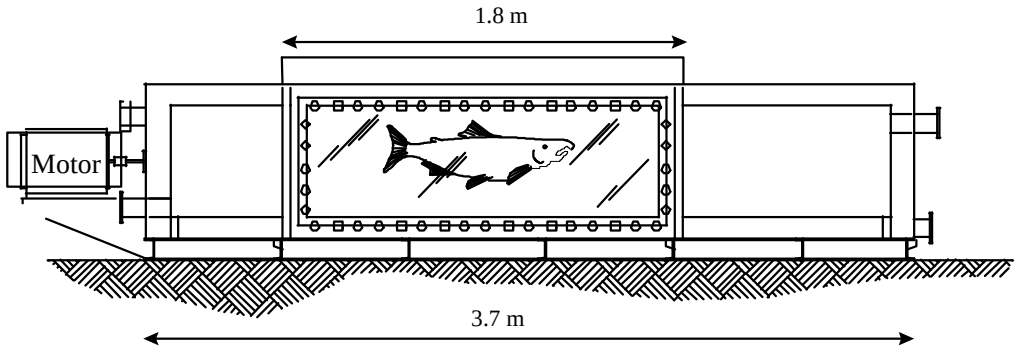
Respirometry Trials

A custom-built 2200-L Brett-type respirometer (Brett 1964) was used to determine the relationship between EMG pulse rate and oxygen consumption. The respirometer was constructed of stainless steel and contained a working section with removable cover, impeller, flow straightener, and viewing window (Figure 4). The working section where fish were exercised measured 1.8 m

long, 53 cm wide, and 53 cm high. A 25-hp variable speed direct-current (DC) motor turned the impeller that provided velocities that ranged from 0 to 150 cm/s. The respirometer unit was immersed in a fiberglass cooling tank that measured 4.5 x 1.7 m. Water temperature could be regulated between 10º C and 23º C. During trials, the respirometer was sealed from the cooling tank so that no gas exchange occurred. An electric screen, designed to keep fish from resting during



Plan view



Side view

Figure 4. Plan and side views of the respirometer used in this study.

trials, was attached to the back panel of the working chamber and delivered a 5-V DC shock if touched by a fish's caudal fin; the shock did not affect the EMG transmission. A temperature probe was installed in the working section through a sealed instrument port.

We conducted 11 tests (four at 15º C and seven at 20º C) during October and November, 1995. All tests were carried out in either 15º C or 20º C water that was a mixture of Columbia River and well water. Individual fish were acclimated to the swimming chamber overnight at low velocity (~30 cm/s). In a few instances, fish were acclimated for 2 hr the same morning as the test. Oxygen-fresh water was allowed to flow through the respirometer during the acclimation period. Following the acclimation period, individual fish were subjected to a series of swimming trials separated by periods of rest (Table 1). The water velocity was adjusted upward slowly (~10 cm/s/min) at the beginning of each trial until the appropriate swimming speed was attained. Once this occurred, the velocity was held constant during the remainder of the trial. Usually, each fish was exercised at water velocities of 30 cm/s (essentially a resting state), 75 cm/s, 105 cm/s, and 135 cm/s; however, individual fish did not always complete the test series. Occasionally, a fish was able to maintain position in a water velocity of ≥ 150 cm/s, although this was rare. Each trial lasted 1 hr or until the fish was so exhausted it could no longer swim or the percent saturation of dissolved oxygen in the respirometer dropped below 75% saturation. At the end of each trial the velocity was adjusted to 30 cm/s, and oxygen-fresh water was allowed to flow through the respirometer. The respirometer was considered re-oxygenated when dissolved oxygen was ≥ 85% saturation.

Table 1. Sample test scenario.

Hour	Swimming Speed
0730 - 0830	Start trial at 30 cm/s
0830 - 0900	Reoxygenation
0900 - 1000	75 cm/s
1000 - 1030	Reoxygenation
1030 - 1130	105 cm/s
1130 - 1200	Reoxygenation
1200 - 1300	135 cm/s
1300 - 1330	Reoxygenation
1330 - 1430	≥ 150 cm/s - usually not needed
1430 - 1500	Reoxygenation - fish moved to pond following inspection and treatment
1500 - 1600	Blank at 30 cm/s
1600 - 1630	Reoxygenation (if necessary)
1630	Place new fish in respirometer at 30 cm/s

Oxygen Consumption and EMG Pulse Rates

We collected oxygen consumption and EMG pulse rate data from seven fish. Four fish were tested at 15º C, and all seven fish were test at 20º C. Oxygen concentrations in the respirometer were determined every 15 min during each trial by means of a YSI dissolved oxygen probe and every 30 min by Winkler method titrations (APHA et al. 1975). If the fish tired or the percent saturation of dissolved oxygen fell below 75%, the oxygen concentration was determined by both methods at trial termination. The average amount of oxygen used by the fish for each trial was determined first by calculating the amount of oxygen depleted. This was done individually for the two sampling methods, and these two values were averaged. In addition, a blank trial was performed after each fish to determine the amount of microbial oxygen use. Fish weights were estimated using a length to weight relationship for Hanford Reach fall chinook salmon (unpublished data, D.R. Geist).

The oxygen consumption rate for an individual fish during a trial was determined using the following equation:

$$O_2 \text{ consumption (mg } O_2 \text{ / kg fish wt / hr)} = \frac{\left(\dfrac{\text{avg. } O_2 \text{ used by fish times the volume of respirometer}}{\text{weight of fish}}\right)}{\left(\dfrac{\text{trial length}}{1 \text{ hr}}\right)}$$

EMGs were recorded continuously during each trial and averaged for the duration of the trial (usually 1 hr). EMG recordings were converted from pulse intervals into pulse rates (pulses/min). EMGs were not recorded during the resting period.

Data from only those trials where we obtained both EMG recordings and oxygen consumption values were used in the analysis. Our experimental design usually resulted in three or four observations of EMG pulse rate and oxygen consumption per fish for each temperature tested.

Fish were grouped by size class, > 90 cm and $\leq$ 90 cm FL, to determine if size-related difference in oxygen consumption occurred. One-way analysis of variance was used to compare oxygen consumption and pulse rates between fish exercised at different water temperatures (15º C and 20º C), between individual fish, and by size class. Oxygen consumption values were transformed to the natural logs of oxygen to reduce the heterogeneity of the residuals. Correlation analysis was used to describe the relationship between swimming speed (cm/s), average EMG pulse rate (pulses/min), and average oxygen consumption (mg O_2/kg/hr).

Linear regression was used to determine the best-fit model for predicting oxygen consumption as a function of EMG pulse rate. A full model, Model 1, with separate slopes and separate intercepts for each size class was compared to two partially reduced models, Model 2, with separate slopes with common intercepts, and Model 3, with common slopes with separate intercepts, using an extra sum of squares F-test:

$$F = \frac{\left(\frac{\text{Full}(MSS) - \text{Reduced}(MSS)}{\text{Full}(mdf) - \text{Reduced}(mdf)} \right)}{\text{Full}(EMS)}$$

where,

F = extra sum of squares F statistic
MSS = model sum of squares
mdf = model degrees of freedom
EMS = error mean square
edf = error degrees of freedom.

If the amount of variance explained by either of the partially reduced models was not significantly different than Model 1 ($\alpha = 0.05$), then the partially reduced model with the smallest mean square error was compared to Model 4, a fully reduced model consisting of common slopes and common intercepts. If all models were equivalent, then the model that provided the greatest biological meaning was selected.

Bioenergetics Model

The long-term goal of this study was to estimate the absolute energy expenditure of adult salmon ascending the Columbia River to spawn. We were not able to conduct a field study to make this estimate. Instead, using a combination of our respirometry data and literature values for chinook salmon, we compared energy available versus energy used by an "average" fall chinook salmon migrating to spawning areas in the Hells Canyon Reach of the Snake River.

It is well established that the energy available at the beginning of an adult salmon's upstream migration is fixed, highly variable between individuals, and primarily a function of stored fats and proteins (Idler and Clemens 1959; Adams and Breck 1990; Brett 1995). We did not measure the amount of fats and proteins for the fish we tested, but instead used values reported in the literature. For example, Greene (1926) reported the percentage of fat and protein in adult chinook salmon (average size 10 kg, standard length of 86 cm) from the Columbia River at the beginning of their spawning migration to be 16.5% and 17.0%, respectively. At the time of spawning, the fish contained 2.6% fat and 13.7% protein. This represented a reduction in energy reserves of about 1,370 kcal/kg (assuming standard energy conversion rates of 8.7 kcal/g for fat and 4.8 kcal/g for protein; Brett and Groves 1979; Brett 1995). Using data on ovary constituents from Greene (1926), Brett (1995) subtracted from the total energy loss the equivalent energy transferred to reproductive material and estimated that approximately 10,000 kcal would be available for migration for an average sized (i.e., 10 kg) adult chinook salmon. This is the initial energy reserve we used in our model.

For our analysis, we estimated the amount of energy used within a typical reservoir and tailrace/dam and then extrapolated this to the entire migration distance (approximately 800 km) between the mouth of the Columbia River and the Hells Canyon Reach of the Snake River. To do this we made several assumptions, as described below:

- The length of the typical hydropower project was 100 km, with the reservoir portion of the project 95 km and the tailrace/dam portion of the project 5 km.
- Conservative river velocities in the reservoir and tailrace when fall chinook salmon adults are migrating were estimated to be 30 cm/s and 100 cm/s (M. Richmond, PNNL, un-published data).
- Migration rates through the reservoir were 56 km/d (Bjornn et al. 1994; Bjornn and Peery 1992).
- Migration rates in the tailrace/dam were 24 km/d, based on migration rates through free-flowing portions of the river (OFC 1960).

Thus, in order for an adult salmon to make headway upstream at the assumed migration rates, the fish must swim approximately 100 cm/s through the reservoir portion of the project and 135 cm/s in the tailrace. The average time to pass from the forebay of one hydroelectric project to the forebay of the next project with no passage delay was estimated to be approximately 2 days (Bjornn and Peery 1992). We then estimated the energy used for adult fall chinook to pass each project using delay periods ranging from 0 to 10 days.

Our swimming speed-oxygen consumption relationships were used to estimate the amount of oxygen consumed by an adult fall chinook salmon as it migrated and/or held in the reservoir and tailrace. Oxygen units were converted to energy units with the oxycaloric average of 3.25 cal/mg O_2 (Brafield and Solomon 1972).

3.0 Results

Oxygen Consumption and EMG Pulse Rates

Table 2 and Appendix A show oxygen consumption and EMG pulse rate data from seven different fish. Oxygen consumption did not differ between individual fish (P = 0.671), between temperatures (P = 0.391), or between size classes (P = 0.535), and was positively correlated with swimming speed for both size classes (small fish: r = 0.68, P = 0.004; large fish: r = 0.84, P < 0.0001; Figure 5).

Table 2. Average oxygen consumption and EMG pulse rates for seven adult fall chinook salmon tested in a respirometer at 15º C and 20º C.

	Number of data points (number of fish)	Average oxygen consumption rate, mg O_2/kg/hr (standard deviation)	Average EMG pulse rate, pulses/min (standard deviation)
Fish at 15º C	15 (4)	222.7 (101.1)	39.6 (8.0)
Fish at 20º C	22 (7)	253.7 (109.7)	39.5 (6.2)
All fish	37 (7)	241.1 (106.0)	39.5 (6.9)

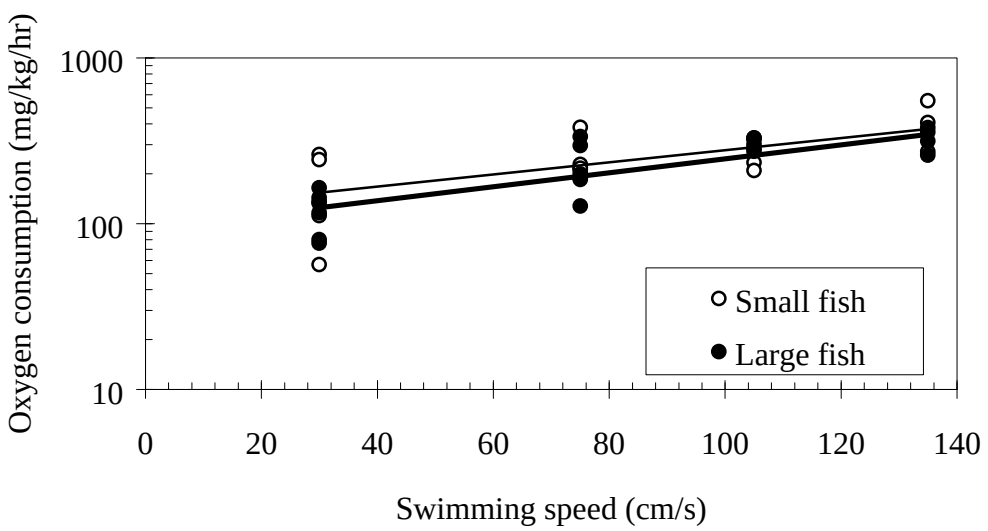


Figure 5. Relationship between oxygen consumption and swimming speed in a respirometer for three small (≤ 90 cm FL) and four large (> 90 cm FL) adult fall chinook salmon at 15º C and 20º C.

The EMG pulse rates did not differ between temperatures tested (P = 0.974) but did differ between individual fish (P = 0.003). Smaller fish (≤ 90 cm FL; average weight 6.3 kg) had a greater pulse rate than did larger fish (> 90 cm FL; average weight 11.5 kg) even though the amount of oxygen consumed was similar (Table 3). The EMG pulse rates were positively correlated with swimming speed (Figure 6) for both size classes (small fish: r = 0.67, P = 0.004; large fish: r = 0.88, P < 0.001).

Table 3. Average oxygen consumption and EMG pulse rate for small (≤ 90 cm FL) and large (> 90 cm FL) adult fall chinook salmon.

	Number of data points (number of fish)	Average FL, cm (standard deviation)	Average oxygen consumption rate, mg O_2/kg/hr (standard deviation)	Average EMG pulse rate, pulses/min (standard deviation)
Small fish	16 (3)	79.2 (8.9)	253.8 (119.8)	44.3 (5.7)
Large fish	21 (4)	98.6 (5.0)	231.5 (96.1)	35.8 (5.3)
All fish	37 (7)	90.3 (12.1)	241.1 (106.0)	39.5 (6.9)

Linear regression analysis of the transformed oxygen consumption showed that the amount of variance explained by Model 1 (the full model), was not significantly different from Model 2 or 3 (Table 4). However, the variance explained by Model 4 (the fully-reduced model) was significantly less than either of the partially reduced models (Table 4). The error mean square (EMS) was equivalent for both partially reduced models. The data showed that the EMG pulse rates were significantly different between fish of different sizes but the oxygen consumption rates were statistically similar. This suggested that the rate of oxygen consumption between size classes was not proportional to the EMG pulse rate for both size classes, and that separate slopes would better describe the EMG-oxygen consumption relationships. Because oxygen consumption rates were similar between fish of different sizes, the rate of oxygen consumption for each size class would be similar as the EMG pulse rate approached zero. A common intercept would appropriately describe the EMG-oxygen consumption relationship of the two size classes. Therefore, Model 2 was selected as the "best-fit" model (Figure 7) and took the form of (standard errors of coefficients are shown in parentheses):

$$\ln (O_2) = 2.18\ (0.30) + 0.088\ (0.01)\ X_1\ I_1 + 0.073\ (0.01)\ X_2\ I_2$$

where:

ln (O_2)	=	the transformed oxygen consumption rate (mg O_2/kg/hr)
X_1	=	the EMG pulse rate (pulses/min) for large fish
X_2	=	the EMG pulse rate (pulses/min) for small fish
I_1	=	the indicator variable designating the size class membership (I_1 = 1 if fish > 90 cm, 0 if not)
I_2	=	the indicator variable designating the size class membership (I_2 = 1 if fish ≤ 90 cm, 0 if not).

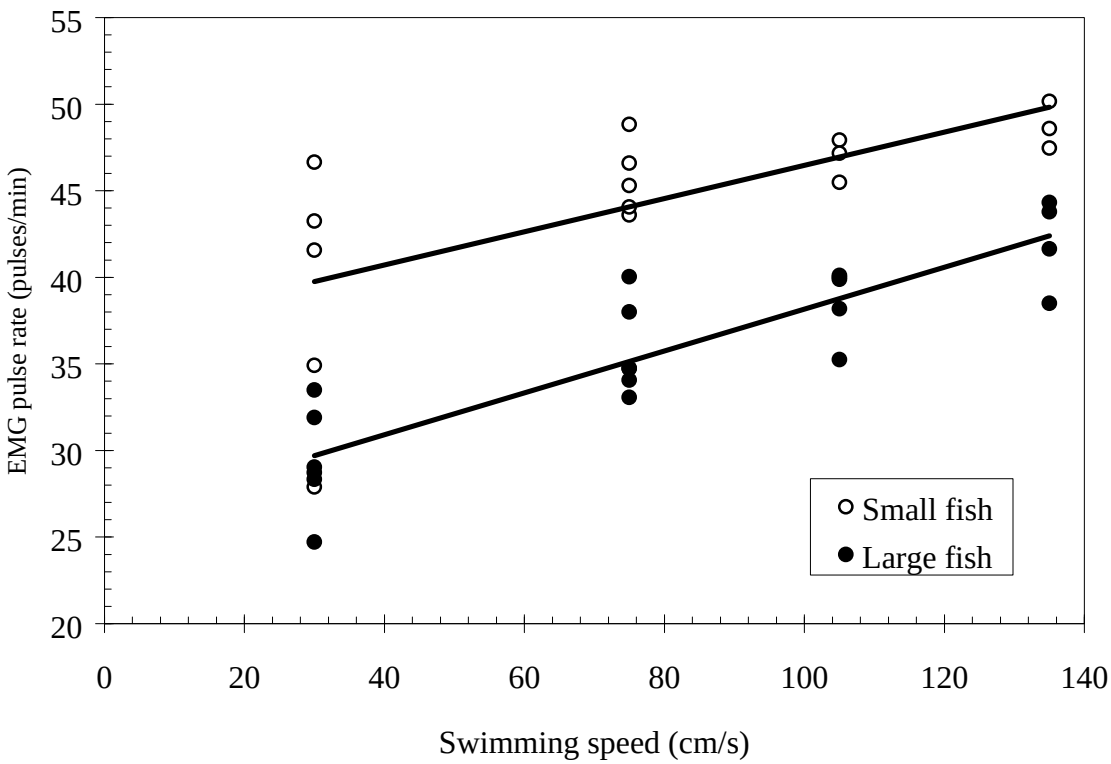


Figure 6. Relationship between EMG pulse rate and swimming speed in a respirometer for three small (≤ 90 cm FL) and four large (> 90 cm FL) adult fall chinook salmon at 15º C and 20º C.

Each increase in one EMG pulse/min is associated with an 8.8% increase in ln (O_2) within large fish (95% CI = 7.1 to 10.5%) and a 7.3% increase in ln (O_2) within small fish (95% CI = 5.9 to 8.7%).

Table 4. Linear regression results between transformed oxygen consumption (dependent variable) and EMG pulse rate (independent variable). Models 2, 3, and 4 were compared to Model 1 using the F statistic (see methods). P-values for the F statistic > 0.05 implied no significant difference from the full model.

		Individual Models			Model Comparisons	
Model Number	Description	EMS[a]	R^2	P-value	F statistic	P-value
1.	Separate slopes, separate intercepts (full model)	0.06	0.77	< 0.0001	-	-
2.	Separate slopes, common intercepts (best-fit model)	0.06	0.77	< 0.0001	0.598	0.45
3.	Common slopes, separate intercepts	0.06	0.77	< 0.0001	0.039	0.84
4.	Common slopes, common intercepts	0.12	0.54	< 0.0001	33.60	<0.0001

[a]EMS = error mean square.

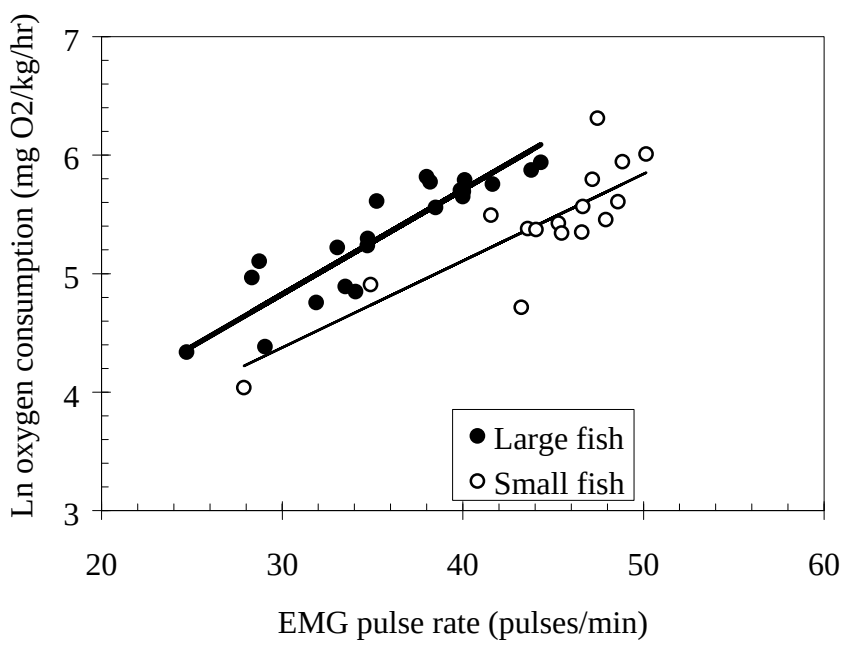


Figure 7. Relationship between oxygen consumption and EMG pulse rate for three small (≤ 90 cm FL) and four large (> 90 cm FL) adult fall chinook salmon at 15º C and 20º C.

Bioenergetics Model

The initial energy reserve available for migration was estimated to be 10,000 kcal (see Methods). Our swimming speed-oxygen consumption relationships (Figure 5) were used to estimate the amount of oxygen consumed by an adult fall chinook salmon as it migrated and/or held in the reservoir and tailrace. We estimated the average adult fall chinook salmon would consume approximately 250 mg/kg/h of oxygen while swimming through the reservoir at a swimming speed of 100 cm/s and approximately 450 mg/kg/h while swimming through the tailrace and over the dam at a swimming speed of 135 cm/s. Energy expended based on these oxygen consumption rates would be approximately 19.5 kcal/kg/d while migrating through the reservoir and approximately 31.2 kcal/kg/d migrating through the tailrace/dam. At a migration rate of 56 km/d, it would take an adult salmon approximately 1.7 days to migrate through the reservoir; this would result in our average fall chinook salmon using 332 kcal of energy in the reservoir. Assuming a migration rate of 24 km/d, it would take approximately 0.2 days to migrate through the tailrace/dam; this would result in 65 kcal of energy being used to migrate through the tailrace and over the dam. Thus, assuming no delay at the dam, the total energy used to migrate through the project was estimated to be approximately 400 kcal. The total use extrapolated over all eight projects was estimated to be approximately 3,200 kcal (Table 5). We assumed that if salmon were delayed at the dam, they would hold in the tailrace area. This would result in approximately 195 kcal of energy used per day. The "extra" energy expended during holding was multiplied by the number of days delayed and added to the energy required for migration (397 kcal) to estimate the total amount of energy used per project (Table 5). This figure was then extrapolated for all eight projects to determine the total amount of energy used during migration through the entire 800 km.

Table 5. Estimated amount of energy used by an average adult fall chinook salmon migrating through a reservoir and tailrace/dam extrapolated to eight projects.

Delay period/project (days)	Energy used per project (kcal)	Energy used for all eight projects (kcal)	Total migration time (days)
0	397	3,176	15
1	592	4,736	23
3	982	7,856	39
5	1,372	10,976	55
7	1,762	14,096	71
10	2,347	18,776	95

4.0 Discussion and Recommendations

Fish Care and Handling

Our ability to collect data for this experiment was hampered by 1) difficulties with fish care and handling, and 2) the failure of some EMG transmitters. Of the 19 fish acquired, only seven survived to the conclusion of the experiment. Six died before being tested, two died while being tested, and four died following one test. All fish died either from injuries received during surgery or from abrasions and fungal infections acquired in the holding pond. Of the 12 EMG transmitters we used, only four worked during both tests. Six transmitters never worked at all, and two worked only during one test.

The fish acquired for this study were nearing the end of their life cycle but were healthy enough to have passed four hydroelectric projects and navigated 80 km of the free-flowing Columbia River. The fish showed advanced secondary sexual characteristics - dark coloration, thickened skin, hooked jaws, receded scales, and mature gonadal development - and because Pacific salmon generally die within two weeks of spawning, we expected some salmon mortality to occur during the study. The majority of the fishes' energy reserves had been depleted and, as they were no longer feeding, there was no means by which to replenish their reserves. Stress resulting from confinement and the inability to spawn in the holding pond, as well as exhaustion from periods of strenuous exercise, contributed to some mortality during holding. All the data reported here were from healthy fish with properly working EMG transmitters, although their physiological performance was likely reduced due to their advanced maturity.

Oxygen Consumption and EMG Pulse Rates

Estimating active metabolism of adult salmon using EMG telemetry has previously been difficult because most respirometers are not large enough to accommodate large adult salmon without impeding fish movement. Consequently, EMG-oxygen relationships have been considered biased and incapable of predicting oxygen consumption of large free-swimming adult salmon (Hinch et al. 1996). This study showed that our respirometer is capable of testing large adult salmon (up to 106 cm FL) over extended periods (i.e., 1 hr). Observations taken during our respirometry trials did not indicate fish movements were impeded. However, it is not possible to conclude that the respirometer did not impede fish movement until EMG pulse rates from free-swimming fall chinook salmon can be compared to laboratory values.

Our respirometry results showed that EMG pulse rates were strongly and positively correlated with swimming speed and oxygen consumption. EMG telemetry has considerable promise for estimating metabolic rates and swimming activity of fish in the natural environment. This conclusion is consistent with other EMG telemetry studies conducted on salmonids (Kaseloo et al. 1992; Hinch et al. 1996), smallmouth bass (*Micropterus salmoides*; Demers et al. 1996), and lake sturgeon (*Acipenser fulvescens*; McKinley and Power 1992).

Oxygen consumption per unit body weight is typically higher for smaller versus larger teleosts (e.g., Brett 1965; Dickson and Kramer 1971; Dewar and Graham 1994). In our study, the smaller size class of fall chinook salmon had slightly lower oxygen consumption rates (but not significantly lower) than the larger (>90 cm FL) size class. One reason for the lack of significant difference in oxygen consumption between size classes was the high variability in oxygen consumption between individual fish. This variability could be due to natural variation in fish response or measurement variability as a result of the large volume of the respirometer. Further testing with larger sample sizes is needed to reduce this variability. Nonetheless, our reported oxygen consumption rates are similar to those found for other salmonids (Figure 8), including those determined from other EMG studies. For example, Hinch et al. (1996) reported that oxygen consumption of sockeye salmon (1.5 to 2.2 kg) during laboratory respirometery experiments ranged from 150.2 to 512.8 mg O_2/kg/hr; our values averaged 253.8 and 231.5 mg O_2/kg/hr for small and large fall chinook salmon, respectively.

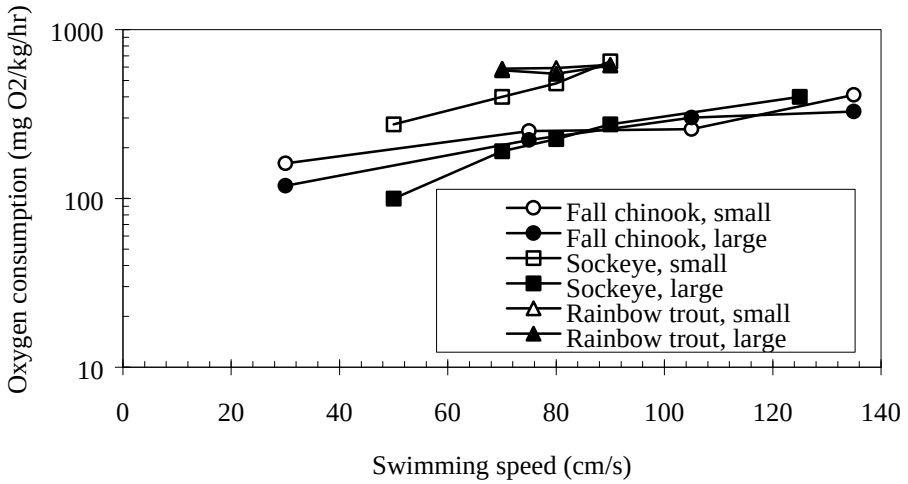


Figure 8. Comparison of oxygen consumption data plotted as a function of swimming speed. Shown are data for small (0.3 kg) and large (1.4 kg) sockeye salmon (Brett 1965) at 15º C, small (0.06-0.1 kg) and large (0.1 to 0.2 kg) rainbow trout (*O. mykiss*; Dickson and Kramer 1971), and our data from small (6.3 kg) and large (11.5 kg) fall chinook salmon averaged for 15º C and 20º C.

EMG pulse rates were significantly faster for smaller fish (≤ 90 cm FL) tested than for larger fish (> 90 cm FL). This is not surprising because EMG pulses are correlated with tail-beat frequency (Wardle and Videler 1993), and tail-beat frequency is usually higher for smaller fish than it is for larger fish (Dewar and Graham 1994). This is because larger fish are more efficient swimmers than smaller fish at high velocities (Dewar and Graham 1994). No other studies specifically reported a relationship between EMG pulse rate and fish length. Most EMG studies have been conducted on small numbers of fish within narrower size ranges. For example, EMG pulse *intervals* reported for adult sockeye salmon (n = 4; 53 to 60 cm FL; wt. = 1.5 to 2.2 kg)

exercised in a laboratory respirometer ranged from 871 to 1,319 ms while EMG pulse intervals observed in the field were commonly recorded from 500 to 800 ms (Hinch et al. 1996). These intervals equate to pulse rates that ranged from 45 to 69 pulses/min in the respirometer, and 75 to 120 pulses/min in the field. EMG pulse rates recorded for smallmouth bass (n = 2; 40.5 and 42.0 cm TL; wt. = 1.05 and 1.26 kg) from a respirometer ranged from approximately 20 to 55 pulses/min (Demers et al. 1996). McKinley and Power (1992) reported EMG pulse intervals for adult lake sturgeon (n = 10; 80 to 95 cm TL; wt. = 4 to 6 kg) in a laboratory respirometer that ranged from approximately 1,000 to 2,100 ms (29 to 60 pulses/min). From these studies it is difficult to identify a clear relationship between fish size and EMG pulse rate.

Model 2, the best-fit model, revealed that the slopes of the regression lines were different for the two size classes, but the intercepts were the same. The similar intercepts would imply little variation between transmitters, electrode placement, and fish size-induced variability in oxygen consumption (Demers et al. 1996). Different slopes suggested that the rate of oxygen consumption was not proportional to the EMG pulse rate between the two size classes. Hence, separate curves for each size class were needed to predict oxygen consumption from EMG pulse rates. For example, the average EMG pulse rates at a swimming speed of 30 cm/s for large and small fall chinook salmon were 30 and 40 pulses/min, respectively (Figure 6). Oxygen consumption predicted at these pulse rates would be approximately 123 mg O_2/kg/hr for large fall chinook salmon (95% C.I. = 73 to 211 mg O_2/kg/hr) and 164 mg O_2/kg/hr for small fall chinook salmon (95% C.I. = 98 to 276 mg O_2/kg/hr). The average EMG pulse rates at a swimming speed of 100 cm/s for large and small fall chinook salmon were 39 and 47 pulses/min, respectively (Figure 6). The oxygen consumption at these pulse rates would be 273 mg O_2/kg/hr for both size classes (95% C.I. = 164.7 to 454.6 mg O_2/kg/hr). Until further data are collected to refine these relationships, two separate regression relationships are needed to predict oxygen consumption based on EMG pulse rate. Because of the low sample size in this study, and the high variability in oxygen consumption, we recommend that further testing of the relationship between EMG pulse rate and oxygen consumption for fall chinook salmon be completed before the regression model presented here be used in a field study.

Bioenergetics Model

A long-term goal of this study was to estimate the absolute energy expenditure of adult fall chinook salmon ascending the Columbia River to spawn. Based on the strong correlation between oxygen consumption and EMG pulse rates for the fish we tested, we believe that EMG telemetry provides a useful approach to estimate energy use of migrating salmon. However, we did not field test this technology, and consequently, were not able to develop a true estimate of energy expenditure for adult salmon. Instead, using a combination of respirometry data and literature values for other salmonids, we developed a conceptual bioenergetics model for an "average" fall chinook salmon migrating to spawning areas in the Hells Canyon Reach of the Snake River.

The initial fat and protein contents (16.5% and 17.0%, respectively) used in our model were taken from mixed chinook salmon stocks from the Columbia River (Greene 1926). Idler

and Clemens (1959) measured adult sockeye salmon (*O. nerka*) adults (2 to 3 kg) from the Fraser River system and found 13.4% body weight was fat and 17.6% body weight was protein at the beginning of the spawning migration. Fat content for Columbia River sockeye salmon was approximately 13% while protein levels were near 20% (Newman and Collins 1967). Rowe et al. (1991) reported a minimum fat content of 12% for adult Atlantic salmon (*Salmo salar*) at the beginning of the spawning migration. Brett (1995) notes that most upriver stocks of Pacific salmon contain greater than 10% fat. Thus, we believe that the values for fat and protein used in our model are reasonable estimates of fat and protein levels in upriver Columbia River fall chinook salmon at the onset of the spawning migration.

In developing our bioenergetics model, we assumed that the majority of energy used by an average adult salmon would be from active, aerobic metabolism (swimming). Our estimates of energy expenditure were conservative because we did not consider other energy uses. Even though fall-back rates of fall chinook salmon may be as high as 15 to 60% at some projects (Monan and Johnson 1974; Mendel et al. 1992, 1994), we did not account for fall-back in our estimates of energy expenditure. Repeated crossing of the dam would result in much higher rates of energy expenditure than reported here. We also did not account for standard metabolism; the amount of energy used during the pre-spawning period once the fish arrived near the spawning areas; or for the amount of energy required for digging and defending redds. This last assumption could significantly affect our results because active metabolism on the spawning grounds equals and in some cases exceeds that for river migration; the average rate increased by 14% for sockeye salmon females and by 59% for males (Brett 1995). This would further deplete an already tight energy budget. Finally, not all the energy used by an adult salmon would be from sustained swimming (i.e., cruising). For example, short swimming bursts may be necessary to navigate difficult passage areas (Hinch et al. 1996), which may exceed aerobic capabilities. Tail-beat frequency during redd cutting by Atlantic salmon exceeded that which could be sustained aerobically (Johnstone et al. 1992). Therefore, methods that estimate active metabolism using aerobically derived relationships (oxygen consumption versus swimming speed) would not capture these occurrences and likely would result in minimal estimates of energy expenditure.

The conceptual bioenergetics model proposed here is very coarse and useful only as a demonstration that difficult passage and/or delay could deplete energy reserves to critically low levels. Based on our analysis, if adult fall chinook salmon are not delayed at the dams or within the reservoirs, the amount of energy consumed would be low relative to the amount available, and they should arrive at the spawning areas with sufficient energy reserves to spawn successfully. However, the amount of energy available is inversely proportional to the length of delay, and delays of 5 days per project would reduce available energy to levels near the minimum level we have assumed necessary for survival (10,000 kcal). Delays of 5 days are not uncommon for fall chinook salmon at most projects (Dauble and Mueller 1993). This suggests that adult salmon reaching spawning areas in the Snake River may not possess a large energy reserve. Until the relationship between energy expenditure and reproductive success is better defined, we cannot determine if reproductive success would be negatively affected from these delays. EMG telemetry appears to be a useful tool to better define this relationship.

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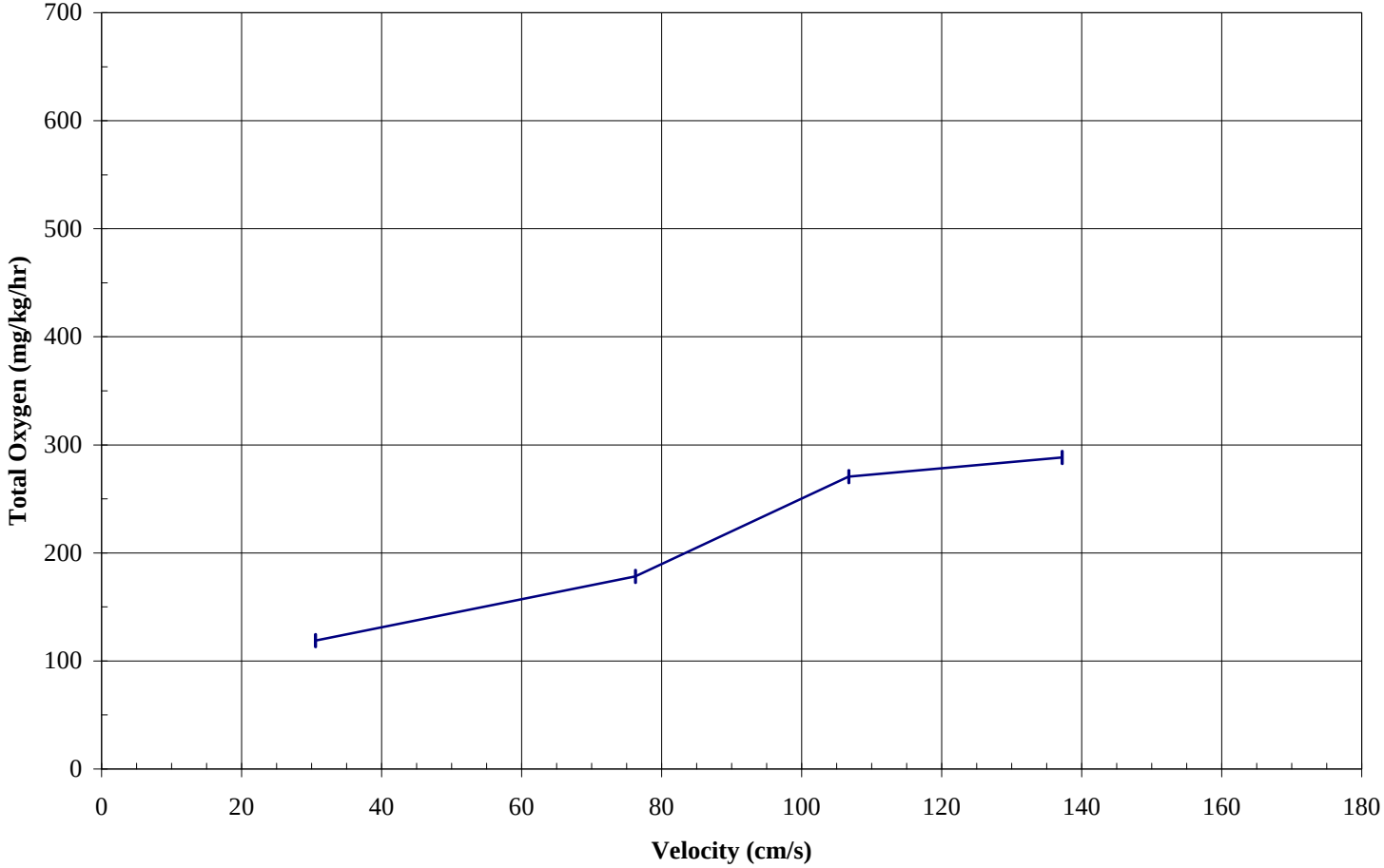
Appendix A

Results of Individual Fish
Swimming Speed vs. Oxygen Consumption and EMG Pulse Rates

Fish #2
Temperature: 20 C



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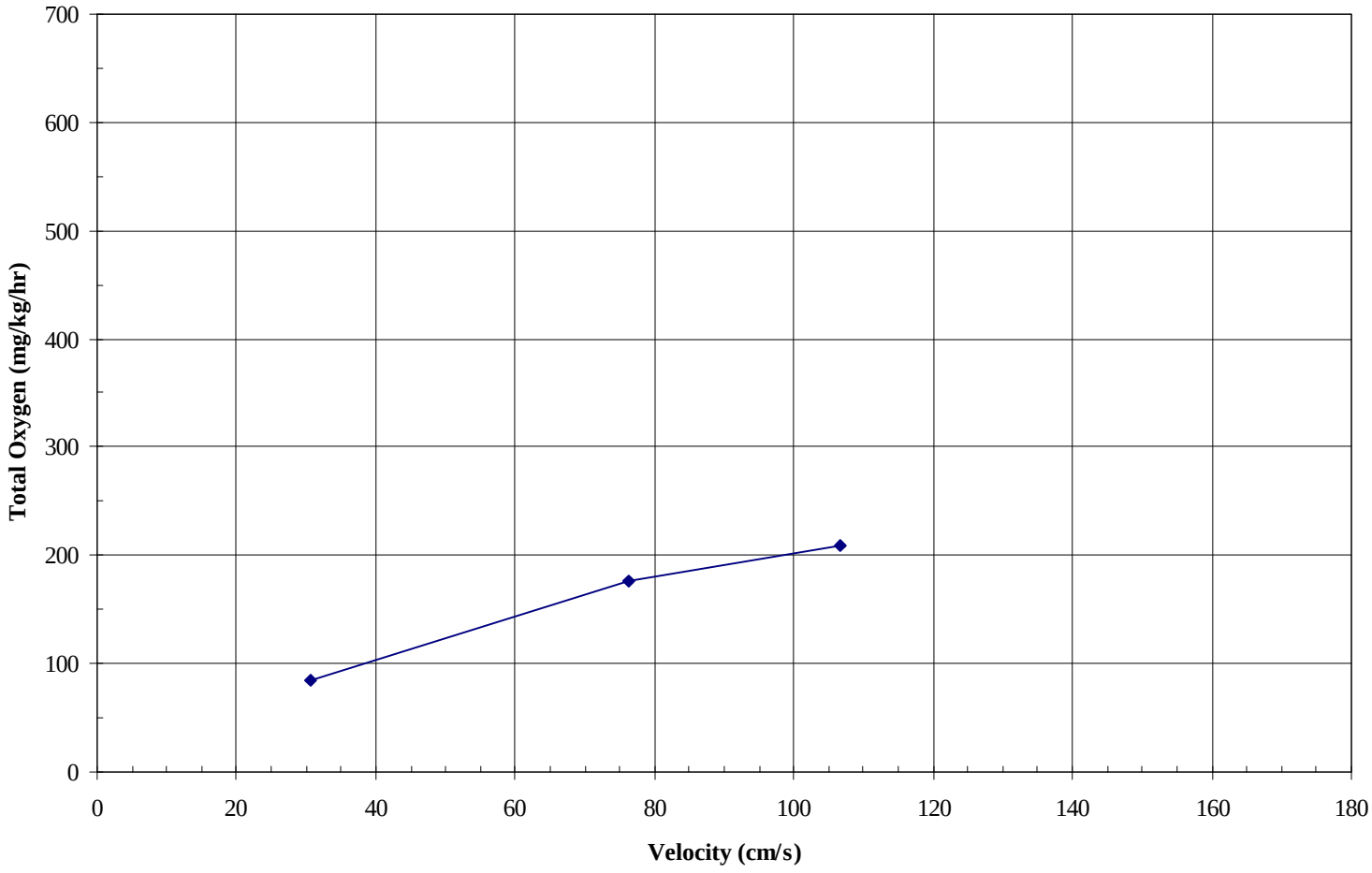

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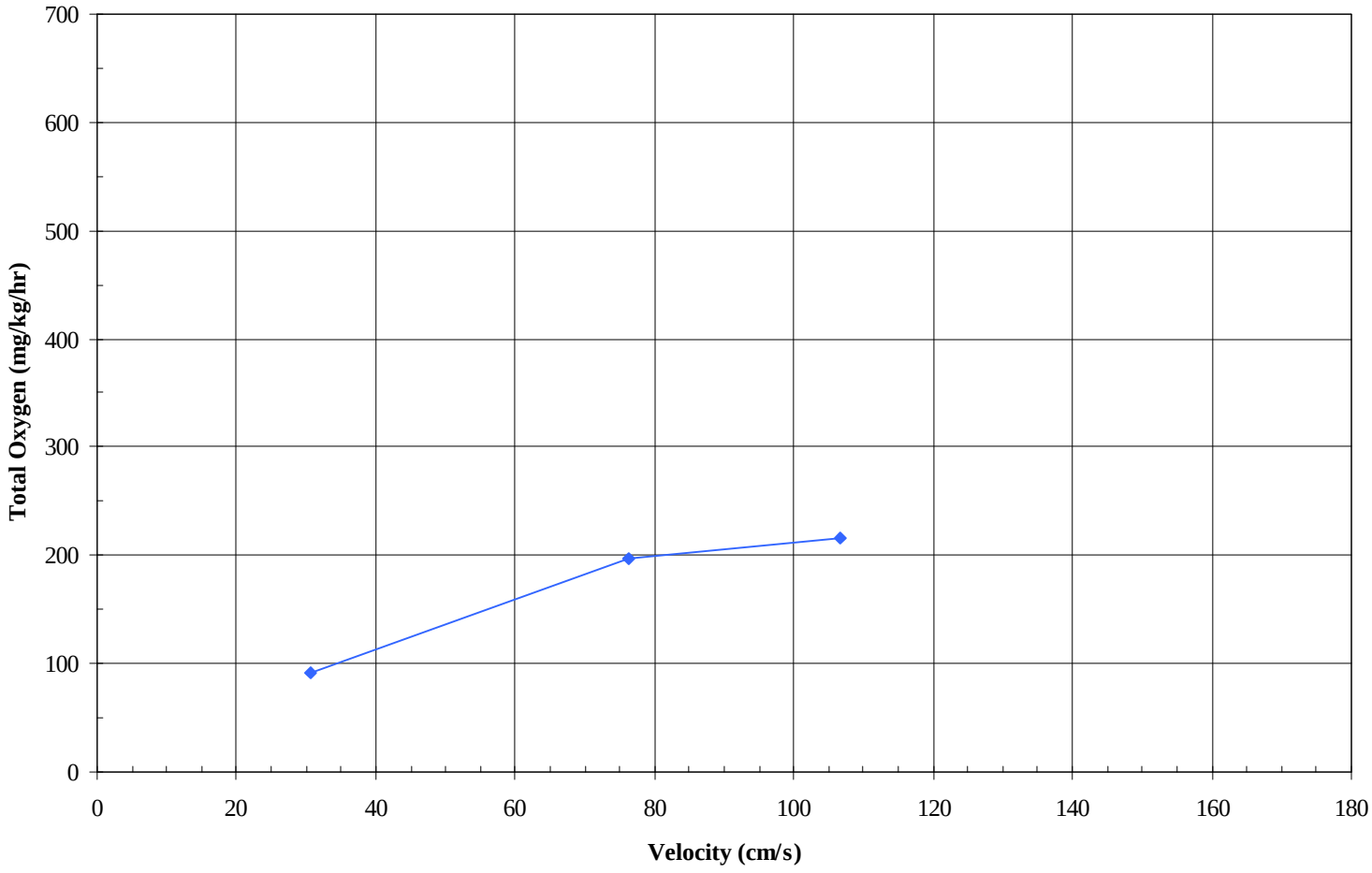

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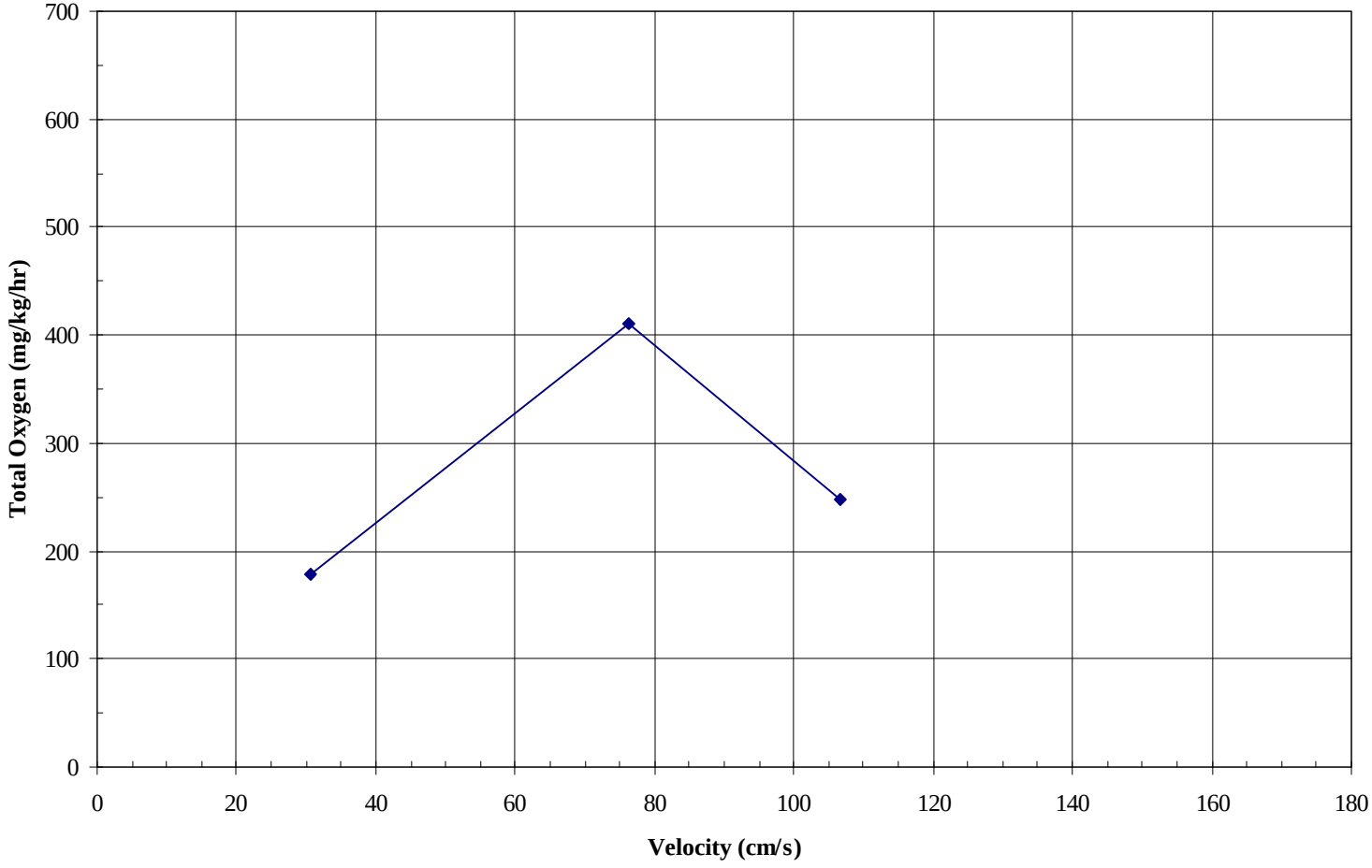

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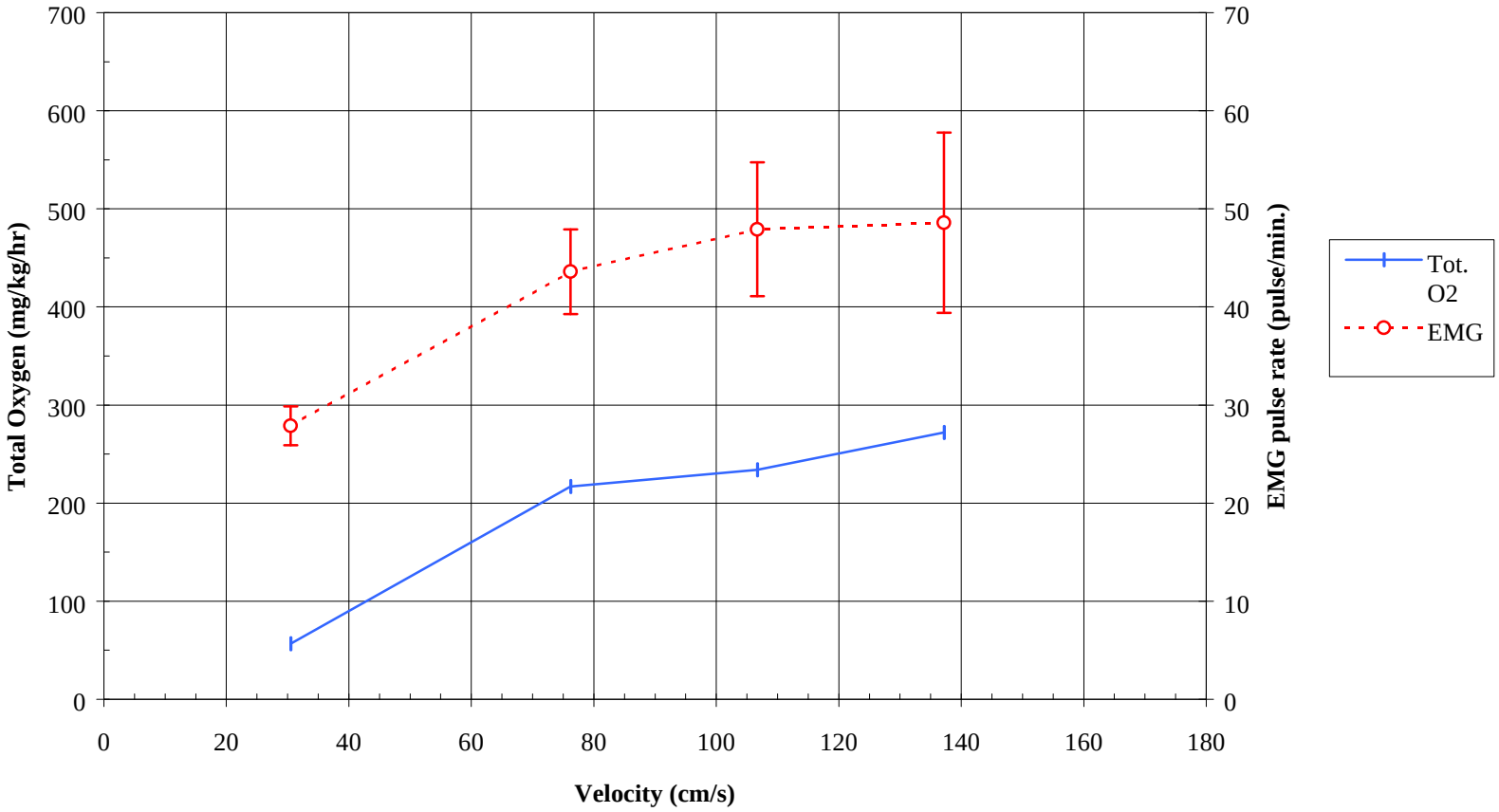

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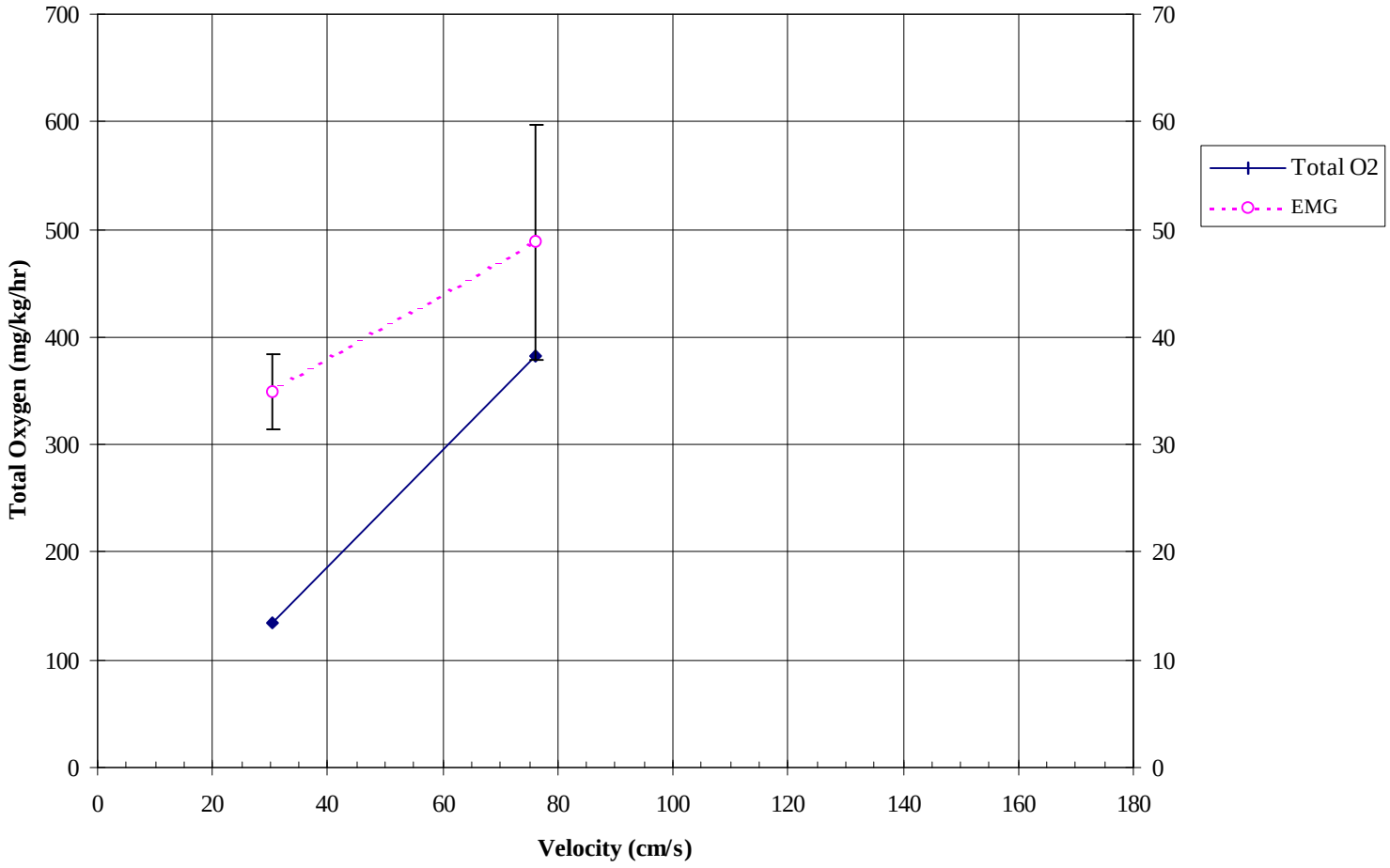

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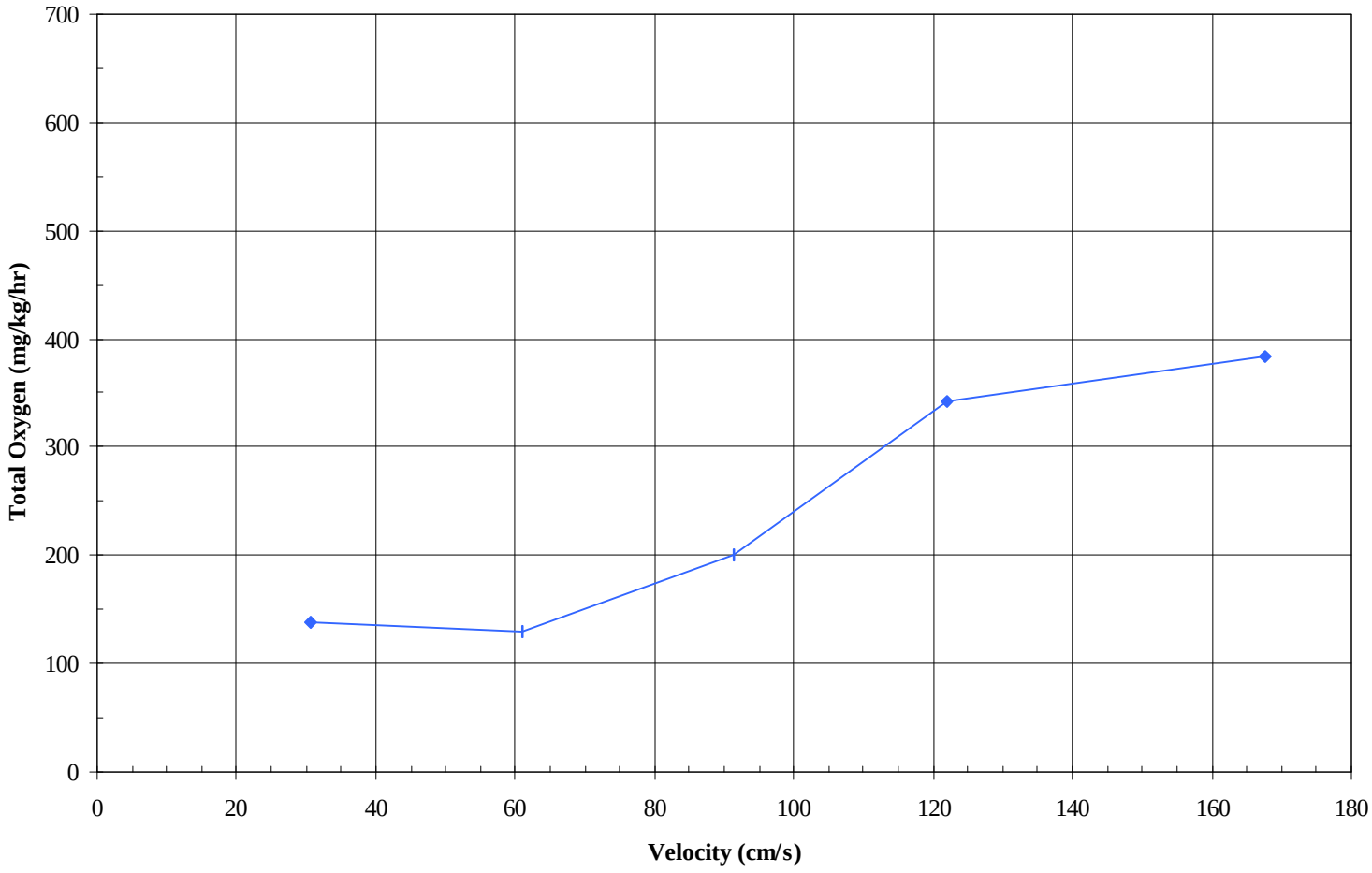

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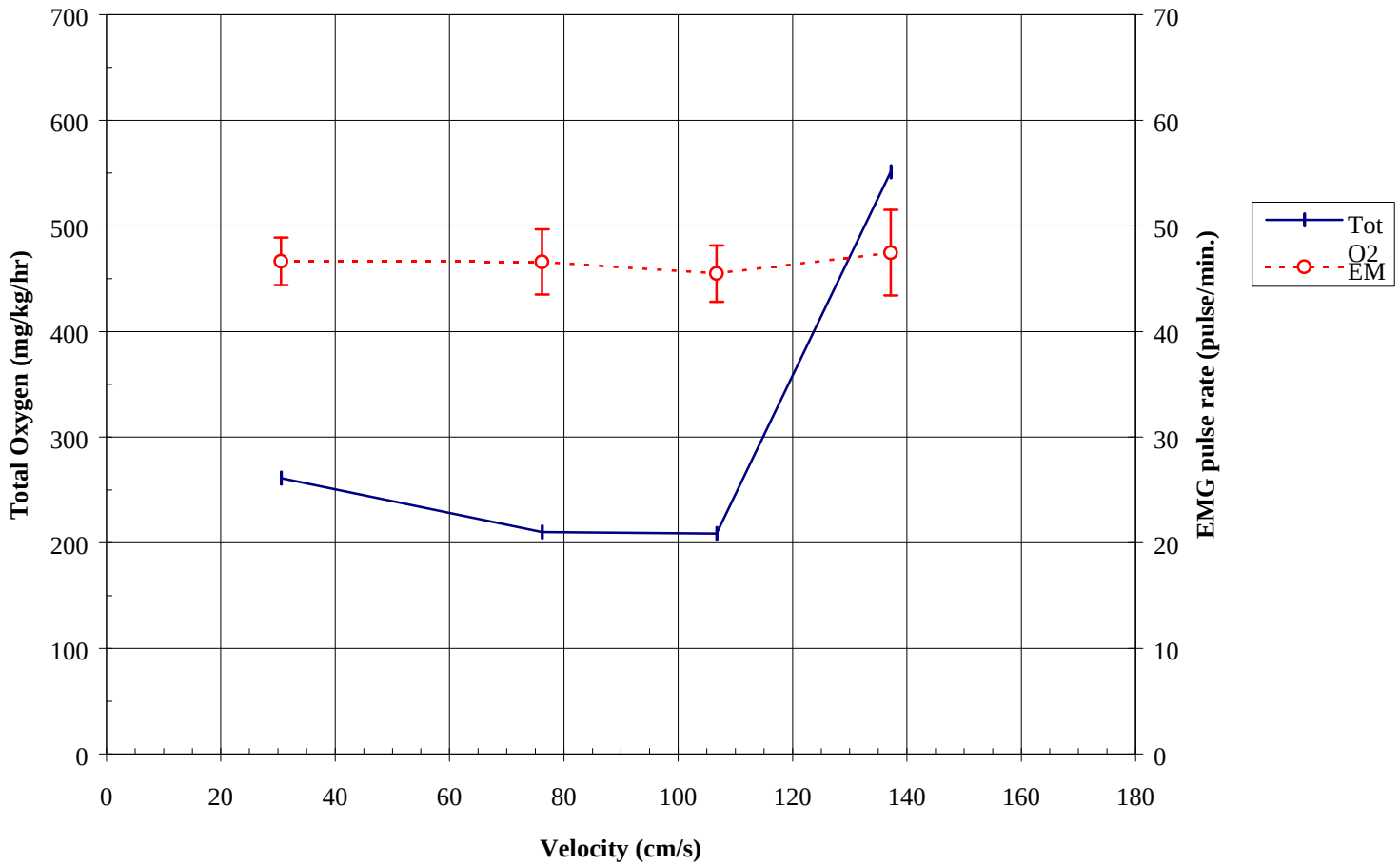

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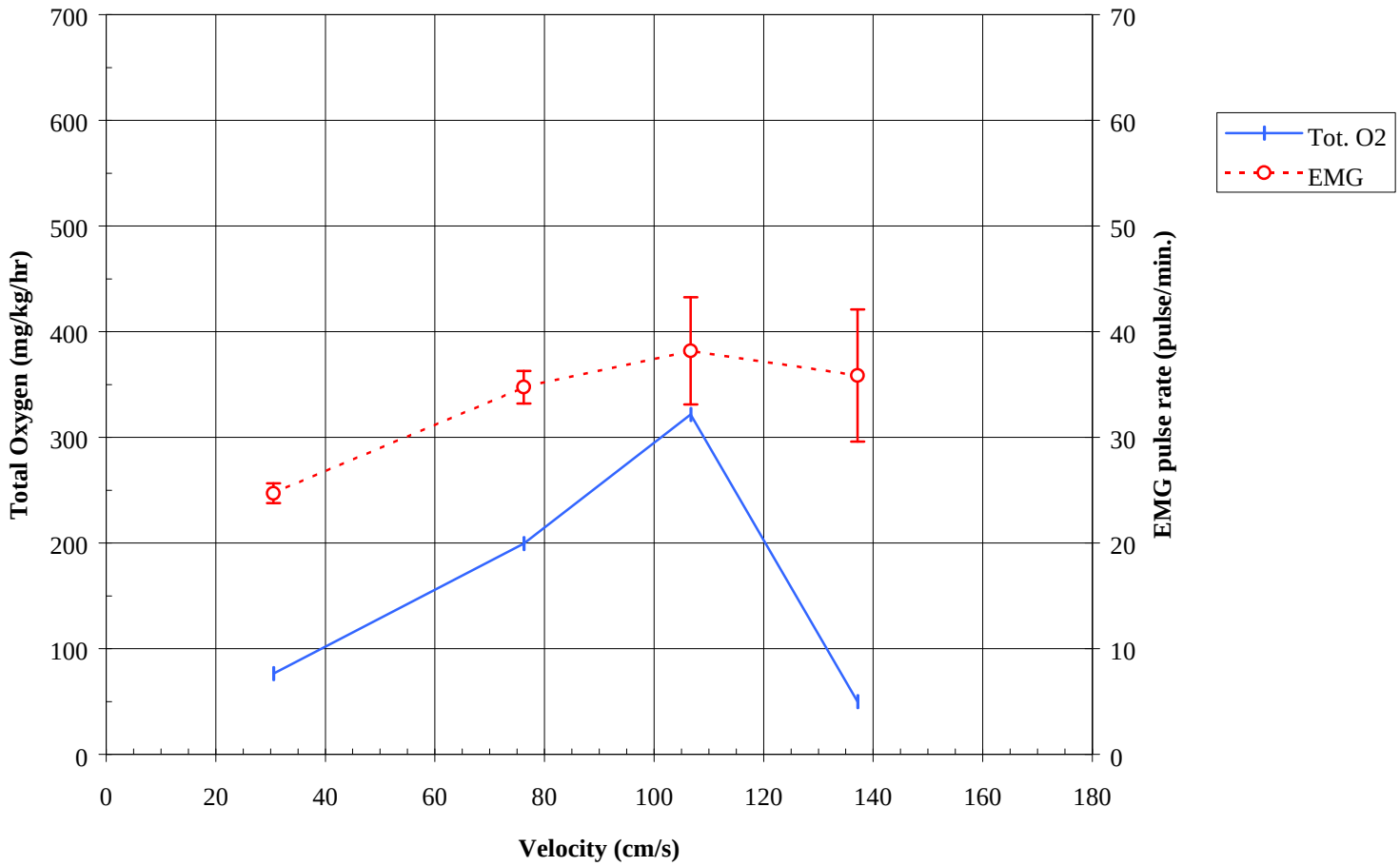

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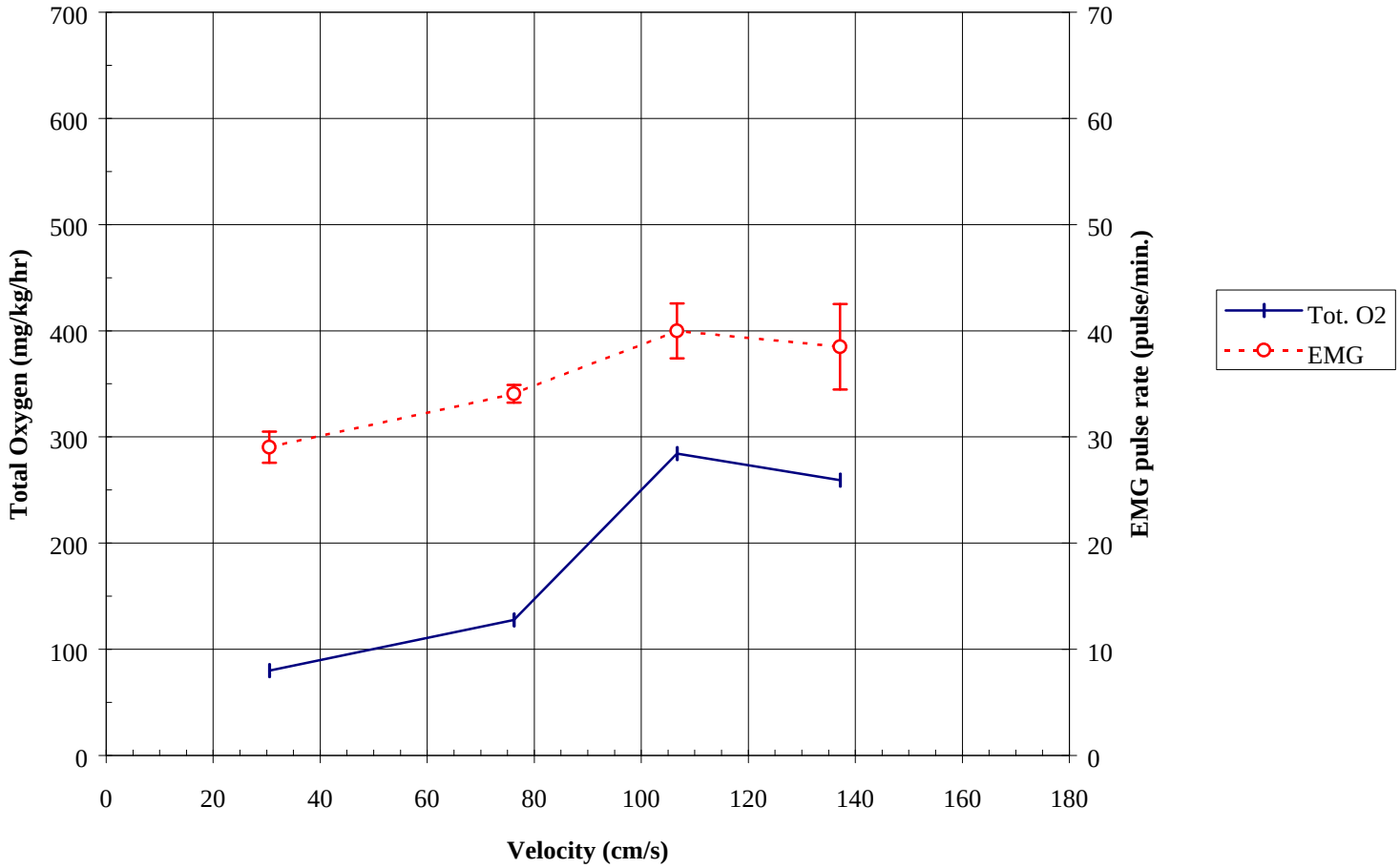

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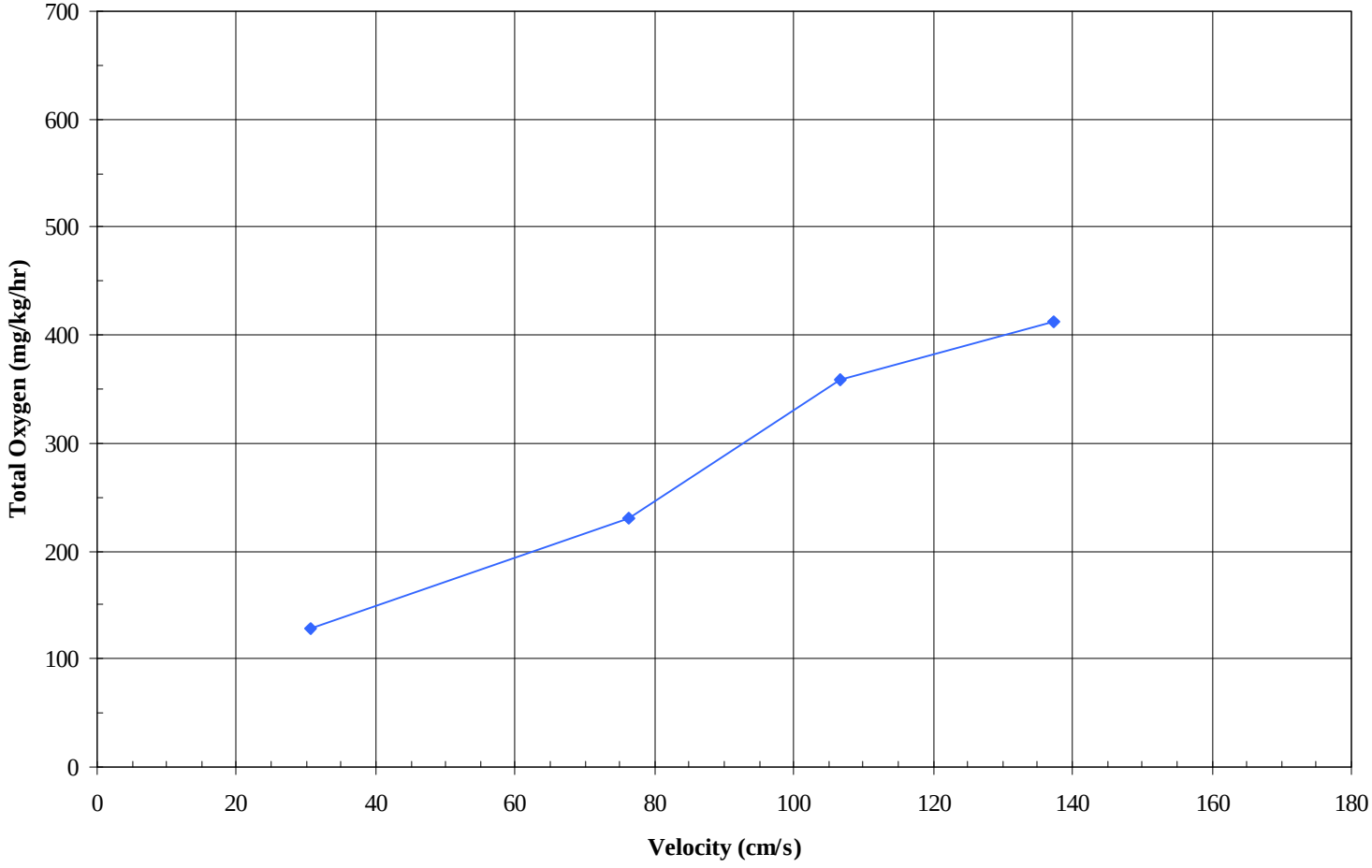

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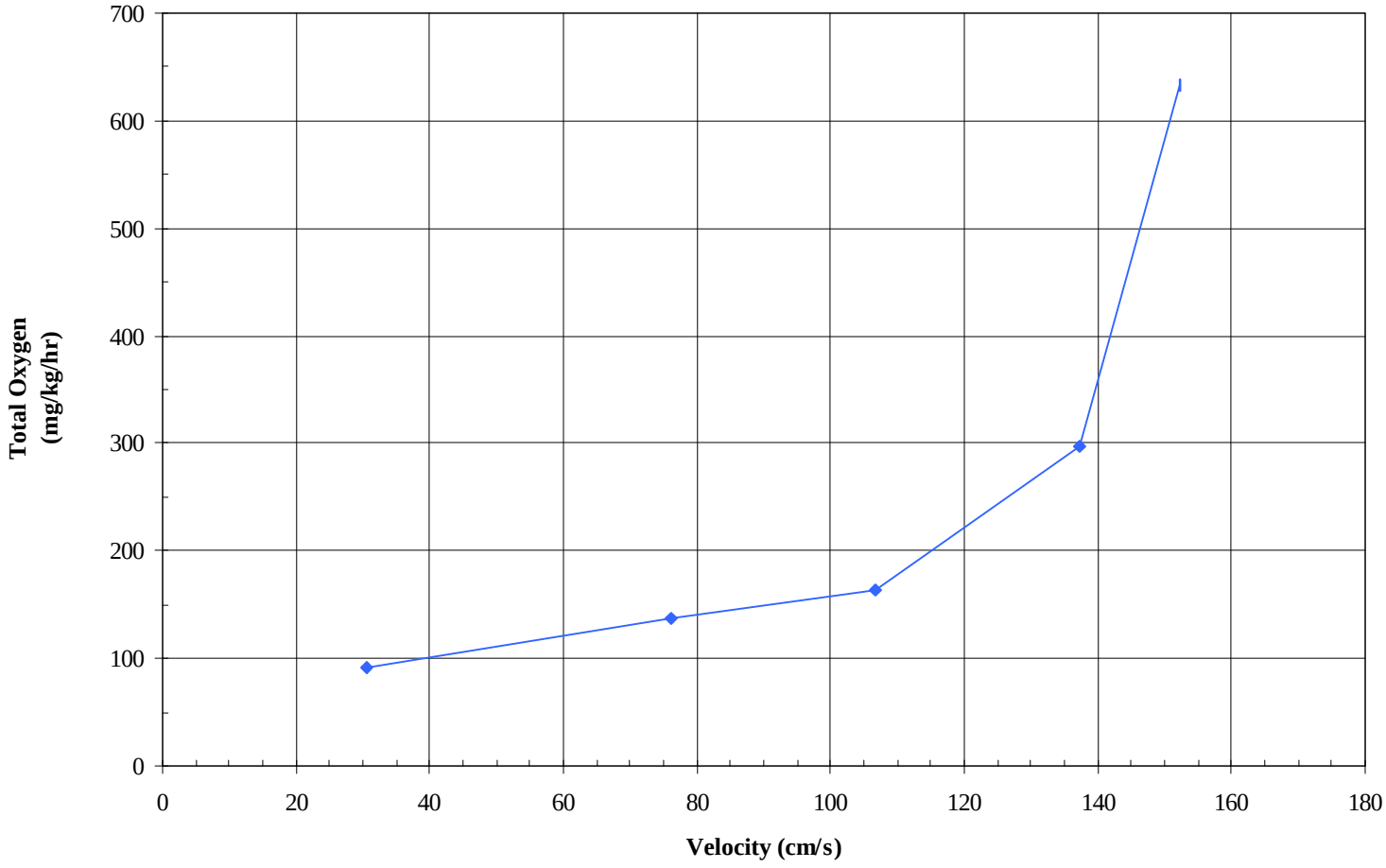
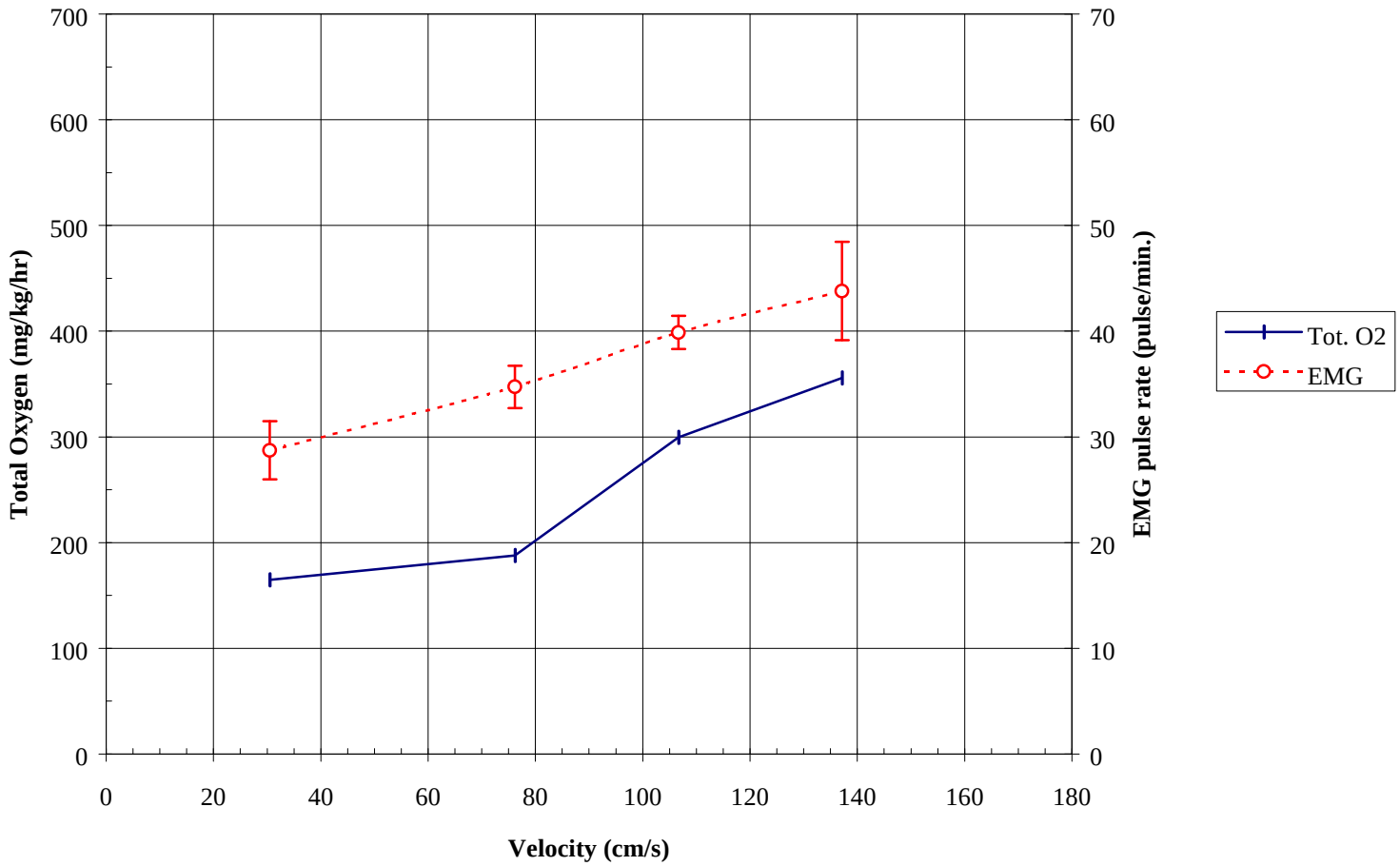
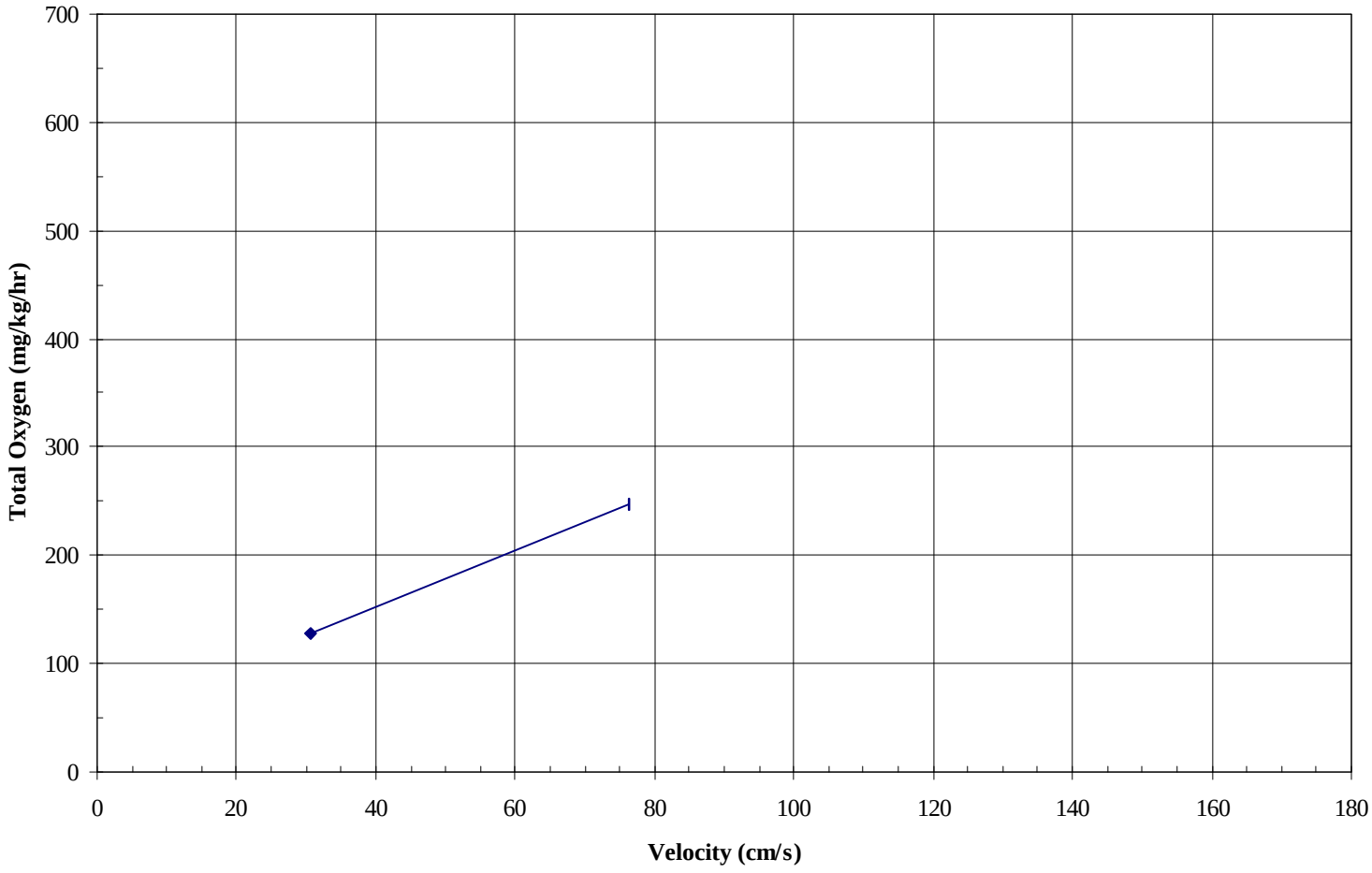


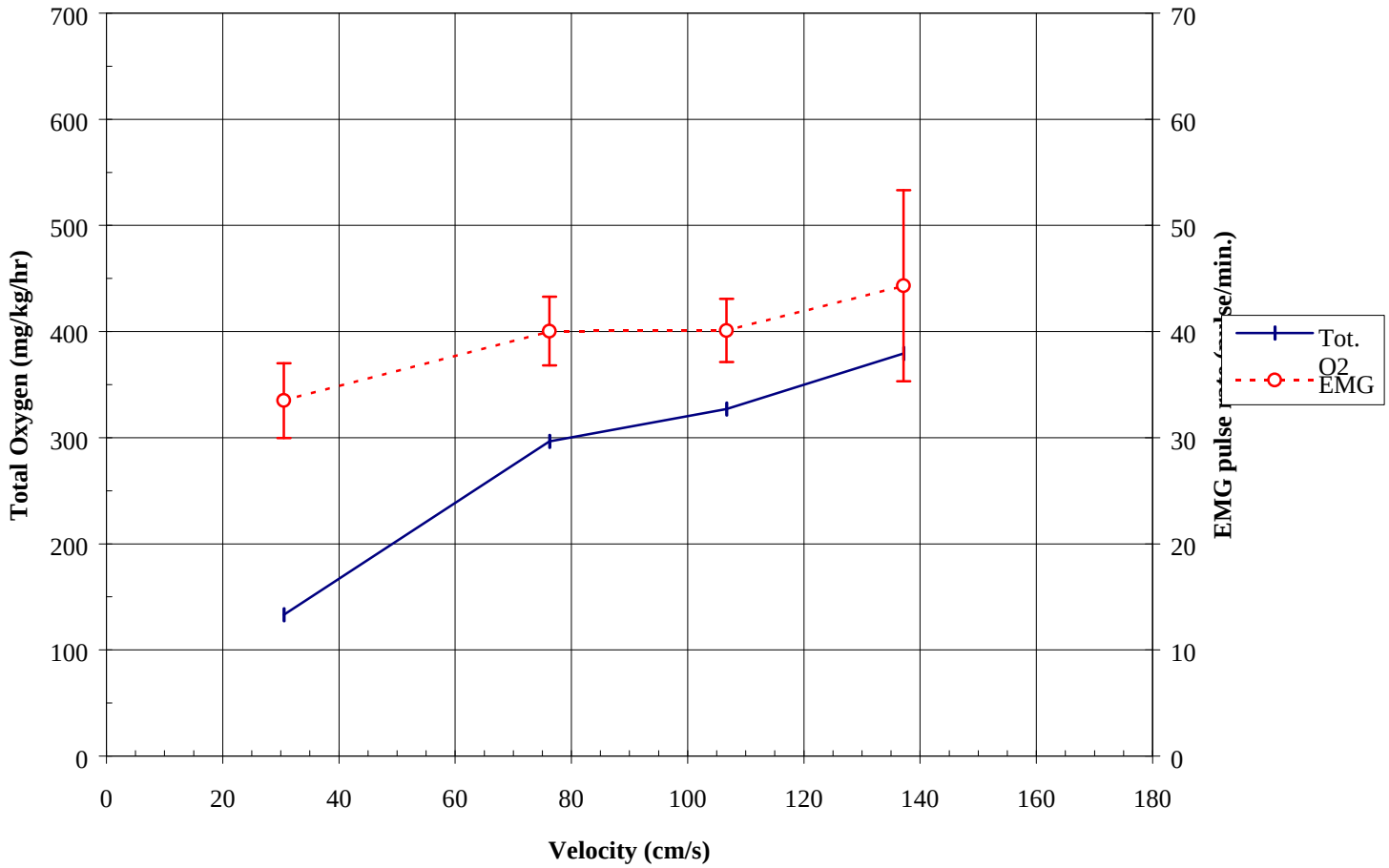
Fish #12
Temperature: 20 C



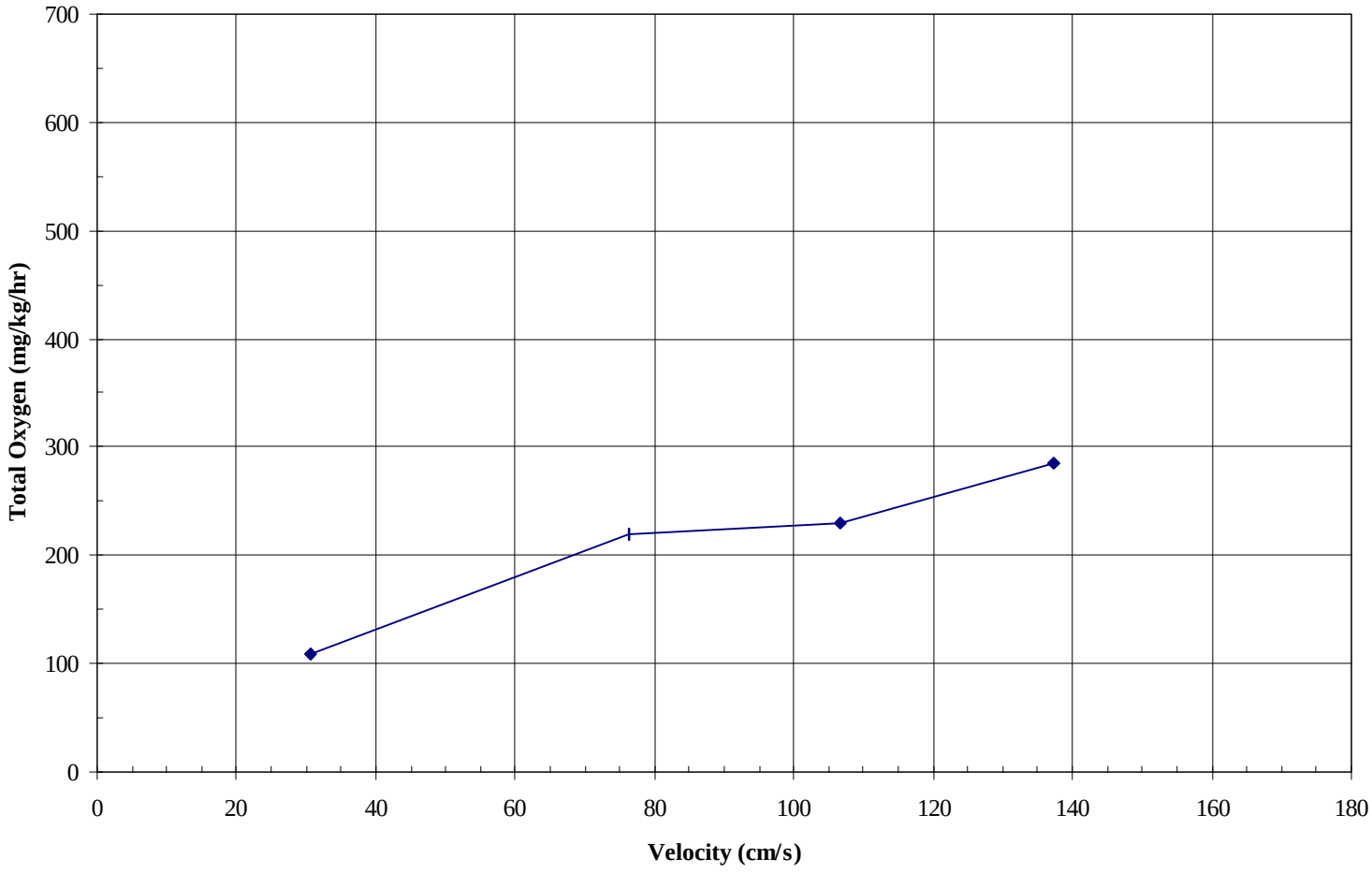
Fish #13
Temperature: 20 C

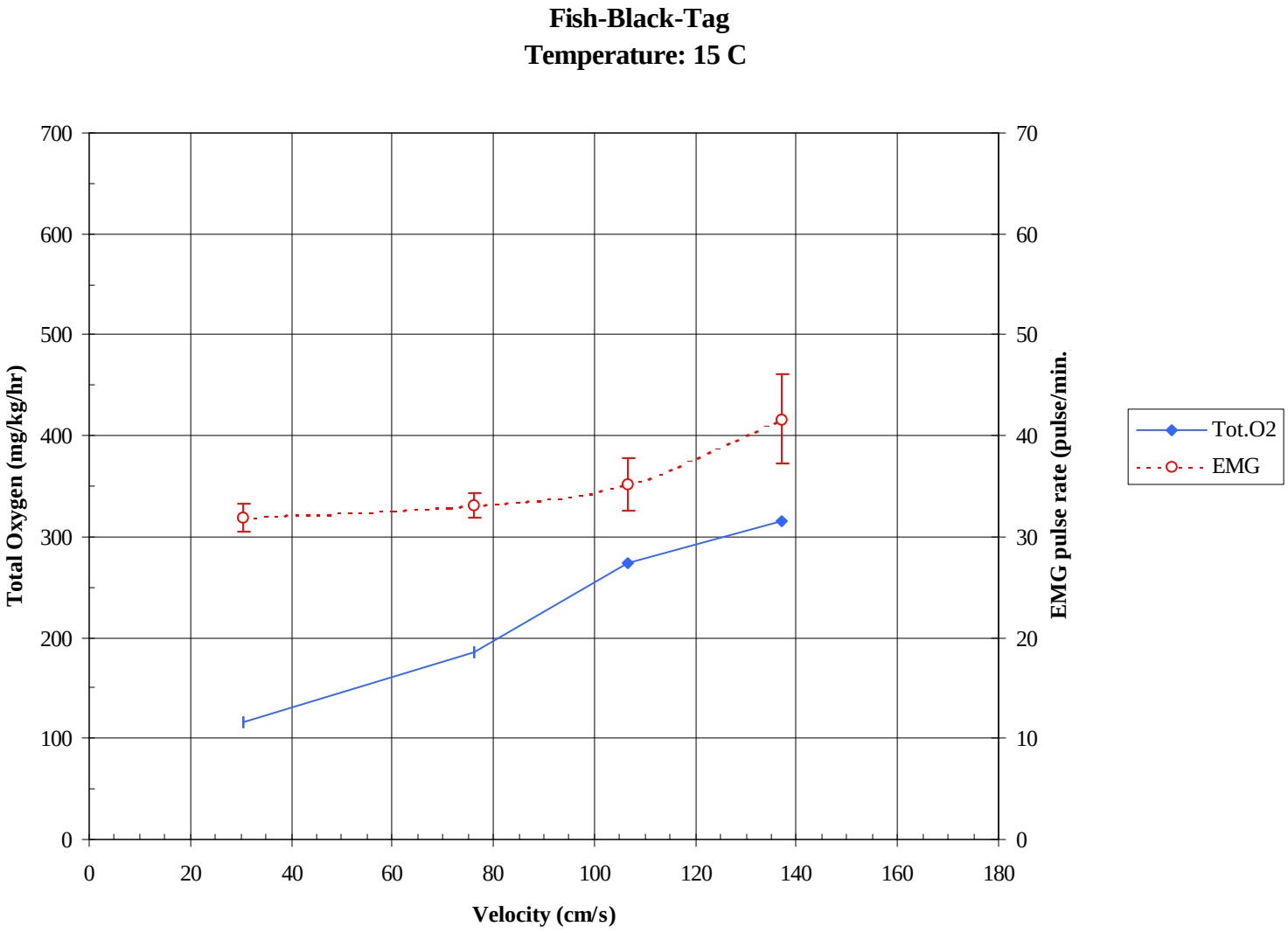


Fish #14
Temperature: 20 C

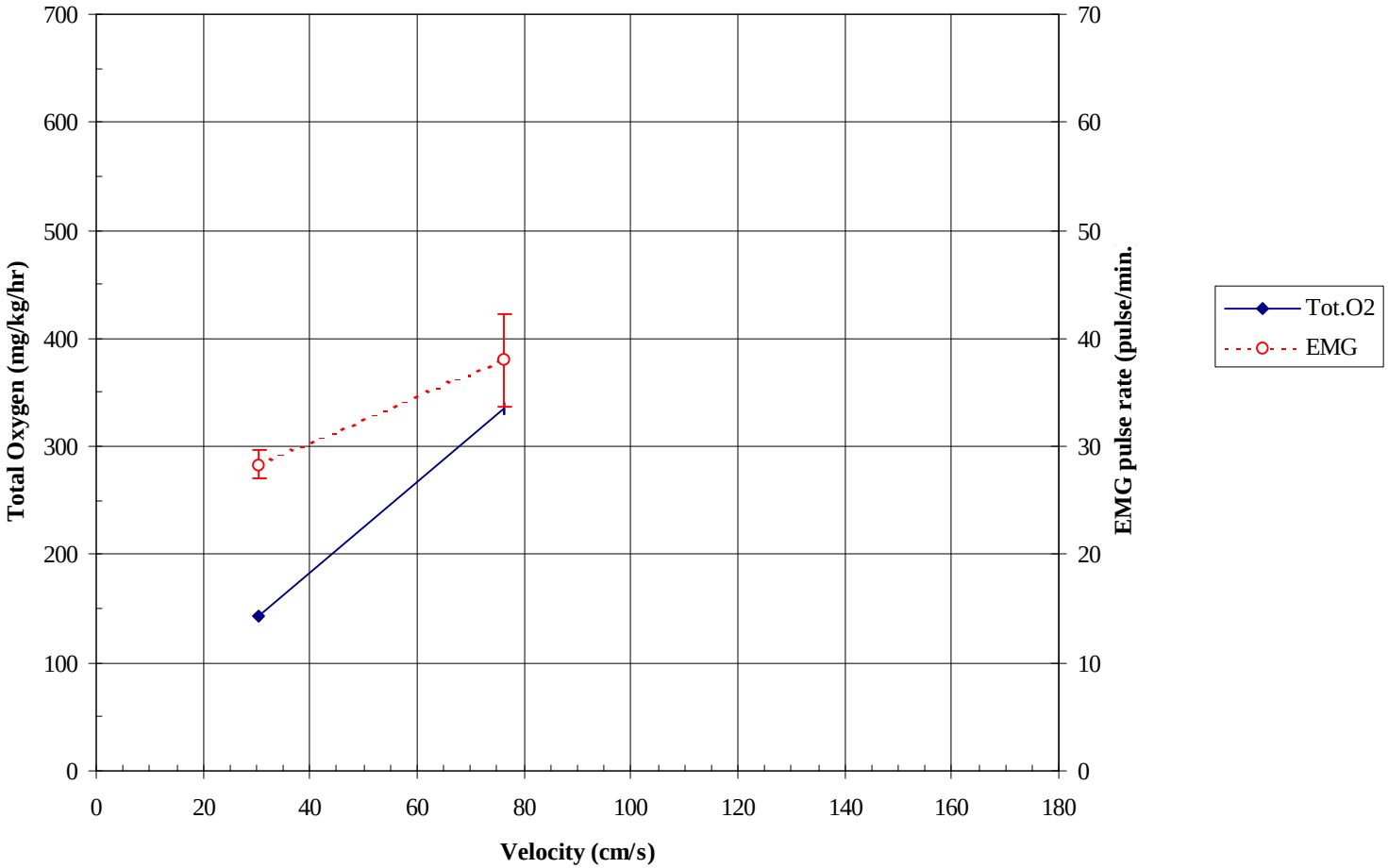


Fish-Black-Ctrl
Temperature: 20C

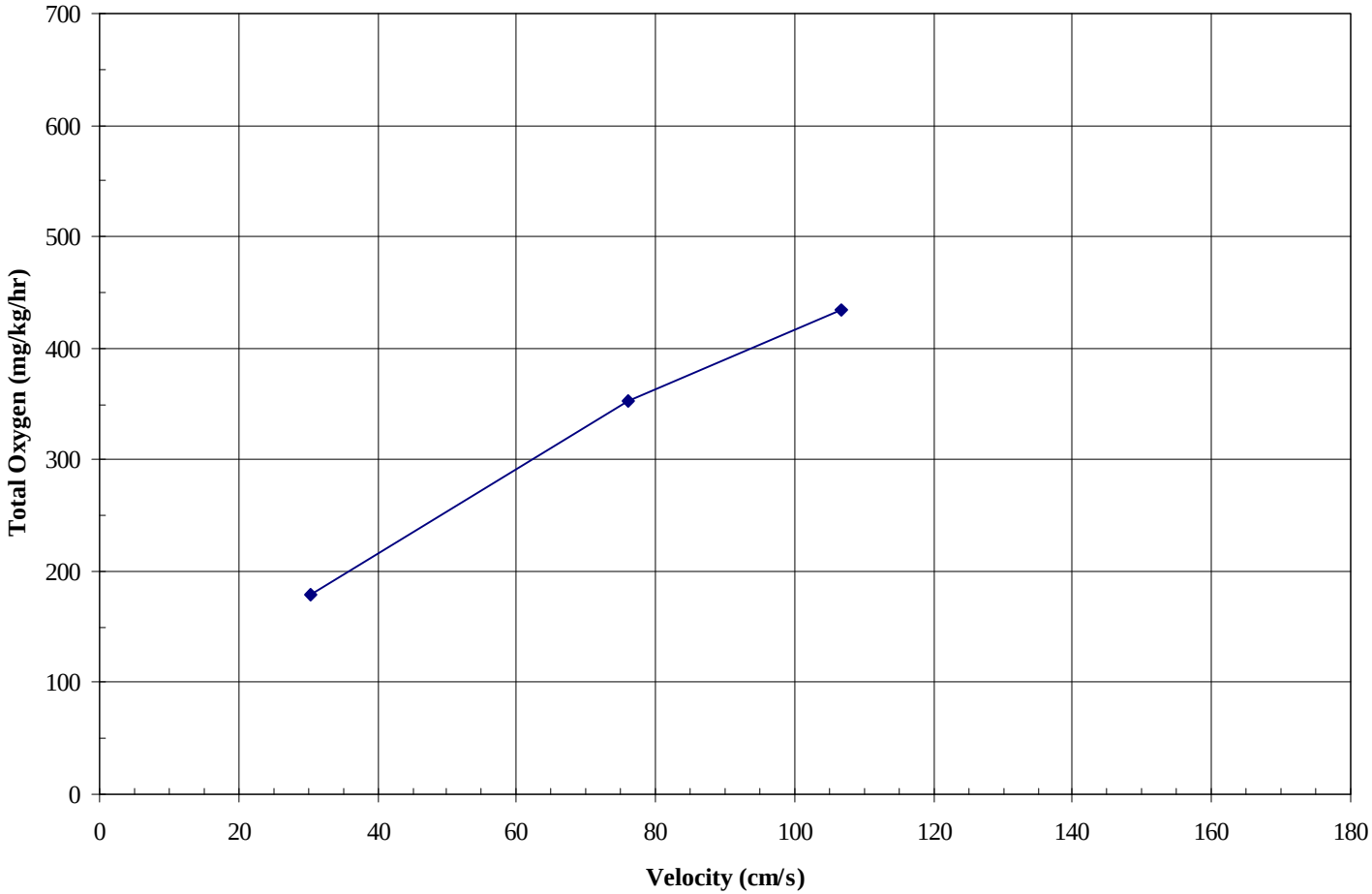



Fish-Black-Tag
Temperature: 15 C
Total Oxygen (mg/kg/hr)
EMG pulse rate (pulse/min.
Velocity (cm/s)
Tot.O2
EMG
0
100
200
300
400
500
600
700
0
10
20
30
40
50
60
70
0
20
40
60
80
100
120
140
160
180

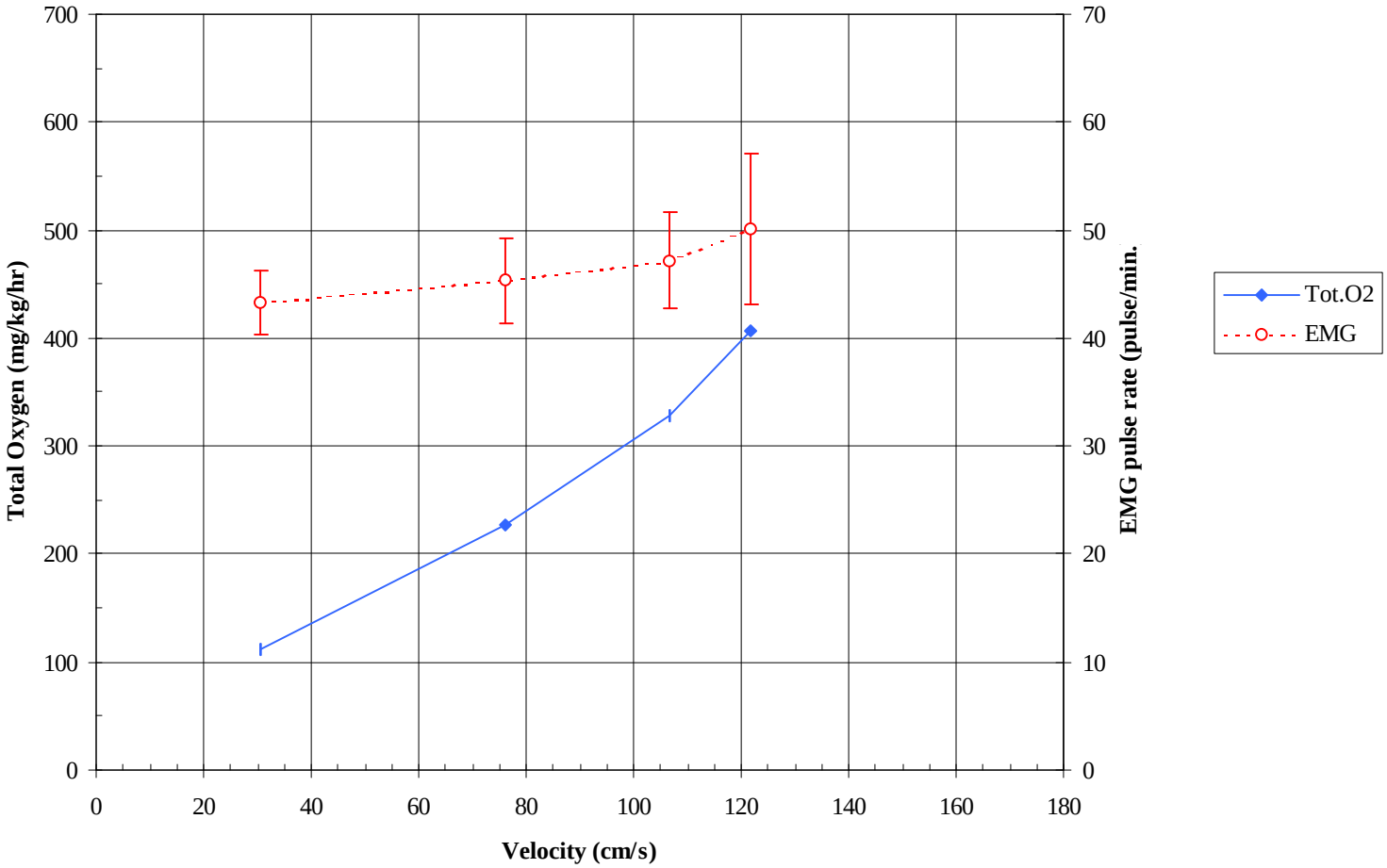
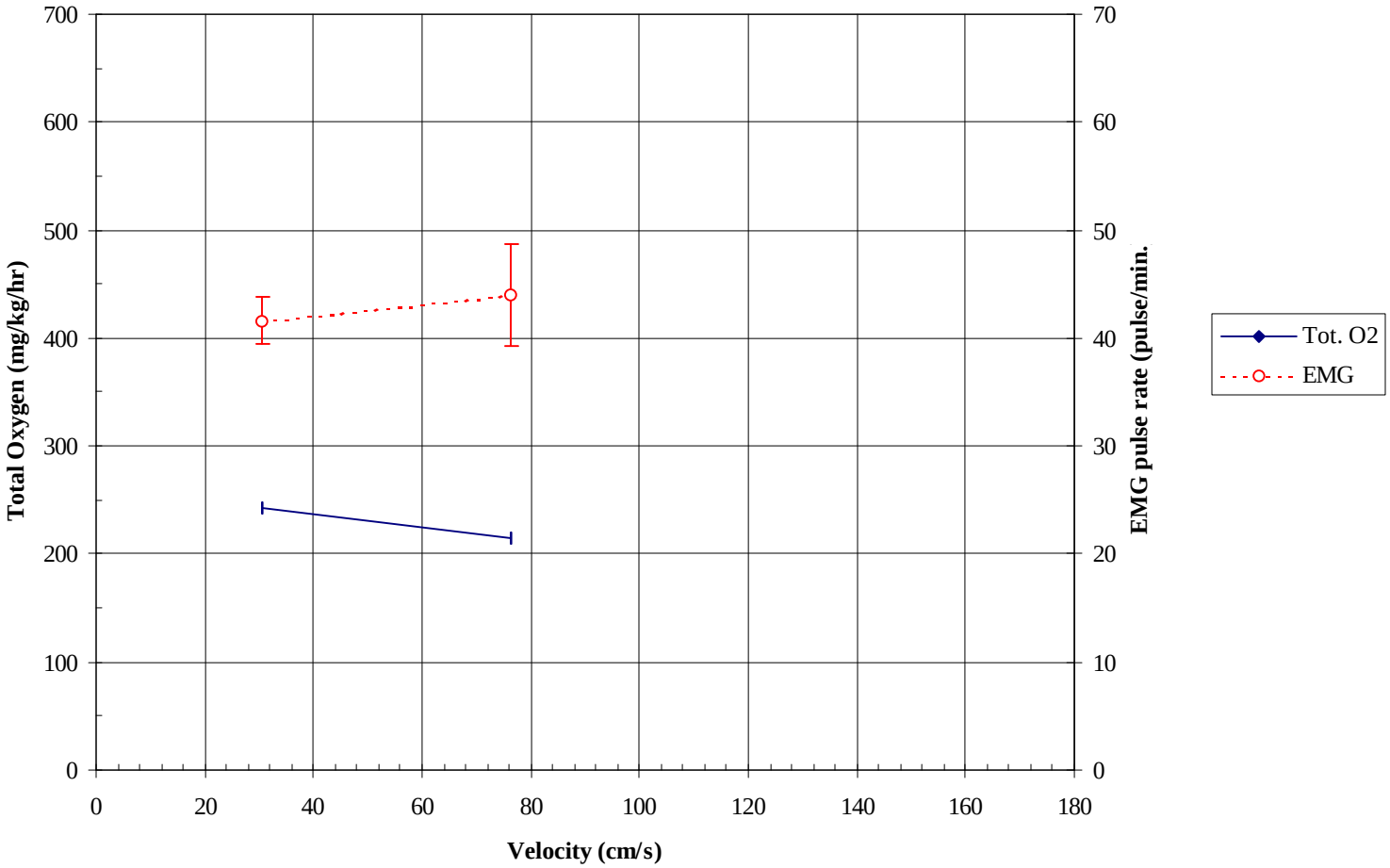
Fish-Black-Tag
Temperature: 20 C



Fish-Red-Ctrl
Temperature: 20 C



Fish-Red-Tag
Temperature: 15 C



Fish-Red-Tag
Temperature: 20 C