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NINA•NIKU  
**PROJECT REPORT**

Radio transmitted electromyogram  
(EMG) signals as indicators of  
physical activity in Atlantic salmon  
(*Salmo salar*)

Finn Økland  
Eva B. Thorstad  
Robert Scott McKinley  
Bengt Finstad  
Richard K. Booth



NINA•NIKU

Foundation for Nature Research and Cultural Heritage Research

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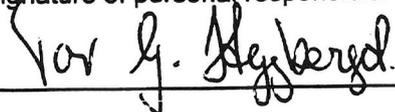
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Contact address:  
 NINA  
 Tungasletta 2  
 7005 Trondheim  
 Tlf: 73 58 05 00  
 Fax: 73 91 54 33

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## Referat

Økland, F., Thorstad, E.B., McKinley, R.S., Finstad, B. & Booth, R.K. 1996. Radiooverførte elektromyogram (EMG) signaler som indikator på fysisk aktivitet hos laks (*Salmo salar*). NINA Oppdragsmelding 002: 1-18.

Målet med denne undersøkelsen var: 1) teste kirurgisk implantering av EMG (elektromyogram) radiosendere i laks (*Salmo salar*), 2) kalibrere EMG pulsintervaller fra rød svømmemuskelatur til svømmehastighet i et svømmehastighetskammer, 3) sammenligne EMG pulsintervaller fra to laksestammer og 4) teste om implanterte EMG sendere påvirker gyteatferd. Totalt 23 laks (10 Lonestamme og 13 lmsastamme) fikk EMG radio sendere implantert i bukhulen. Av disse ble 18 kjørt i svømmehastighetskammeret mens 5 (alle lmsastamme) ble introdusert i en dam med grus og fikk anledning til å gyte. De kirurgiske metodene som ble benyttet i denne undersøkelsen gav 100 % overlevelse i forsøksperioden, og fra 14 av de 18 laksene som ble kjørt i svømmehastighetskammeret kunne vi kalibrere EMG pulsintervaller til svømmehastighet ( $r^2$  fra 0.35 til 0.76 hos enkeltindivider). EMG gjennomsnitt fra alle individene slått sammen, gav  $r^2 = 0.64$  (potenskurve,  $r^2 = 0.64$ ; lineær regresjon,  $r^2 = 0.63$ ). Individuer hadde forskjellige EMG hvilenivå (EMG pulsintervaller registrert på hastighet  $0.5 \text{ ms}^{-1}$ ). Best korrelasjon mellom svømmehastighet og EMG pulsintervaller ble derfor oppnådd ved å korrigere for de ulike hvilenivåene ( $r^2 = 0.75$ ). Det lineære forholdet mellom svømmehastighet og EMG pulsintervaller var signifikant forskjellig mellom de to laksestammene ( $P < 0.05$ ). Én hann og én hunn med implanterte EMG radiosendere gytte, uten at atypisk atferd ble registrert. Hos en annen hunn blokkerte senderen fullstendig for gyting. EMG sendere setter oss i stand til å registrere fiskens aktivitet kvantitativt. Vellykket kalibrering av EMG og svømmehastighet åpner muligheter for å kalibrere EMG til oksygenforbruk, og på den måten måle metabolske kostnader av aktivitet i feltundersøkelser.

Emneord: *Salmo salar* - elektromyogram - radiotelemetri

Finn Økland, Eva B. Thorstad & Bengt Finstad, Norsk institutt for naturforskning, Tungasletta 2, 7005 Trondheim

Robert Scott McKinley & Richard K. Booth, Department of Biology, University of Waterloo, Ontario, Canada. N2L 3G1.

## Abstract

Økland, F., Thorstad, E.B., McKinley, R.S., Finstad, B. & Booth, R.K. 1996. Radio transmitted electromyogram (EMG) signals as indicators of physical activity in Atlantic salmon (*Salmo salar*). - NINA Oppdragsmelding 002: 1-18.

The objectives of this study were: 1) test the surgical methods developed to implant EMG (electromyogram) transmitters in Atlantic salmon (*Salmo salar*) 2) calibrate electromyograms from axial red musculature to swimming speed in a swim speed chamber, 3) compare electromyograms from two stocks and 4) attempt to implant EMG transmitters in spawning salmon. A total of 23 salmon (10 Lone stock and 13 lmsa stock) were equipped with internal EMG transmitters. Eighteen were used in the swim speed chamber and 5 (lmsa stock) released in a pond and allowed to spawn. The surgical procedures worked out satisfactorily, with 100 % survival of all EMG implanted fish during the study. We were able to calibrate EMG pulse intervals to swimming speed in 14 of the 18 salmon run in the swim speed chamber ( $r^2$  between 0.35 to 0.76). When all average EMGs from all individuals were combined, the EMG pulse intervals were slightly better described by a power curve ( $r^2 = 0.64$ ) than a linear regression ( $r^2 = 0.63$ ). Individuals differed in their EMG resting levels (EMGs recorded at  $0.5 \text{ ms}^{-1}$ ), thus a higher correlation was obtained between swimming speed and an activity index (EMG pulse intervals at different speeds / EMG resting levels) ( $r^2 = 0.75$ ). The linear relationship between swimming speed and EMG pulse intervals differed significantly between the two stocks ( $P < 0.05$ ). One male and one female with implanted EMG transmitters spawned in a spawning tank, and the transmitters did not seem to affect spawning behaviour. In another female the transmitter completely inhibited spawning. Successful calibration of EMGs to swimming speed opens the possibility to calibrate EMGs to oxygen consumption and measure the metabolic costs of activity in field experiments.

Key words: *Salmo salar* - electromyograms - radiotelemetry

Finn Økland, Eva B. Thorstad & Bengt Finstad, Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim

Robert Scott McKinley & Richard K. Booth, Department of Biology, University of Waterloo, Ontario, Canada. N2L 3G1.

## Forord

Dette prosjektet har vært et samarbeidsprosjekt mellom Norsk Institutt for Naturforskning (NINA) og University of Waterloo, Canada. Svømmehastighetsrespirometeret som ble brukt i prosjektet, er utviklet og bygd i Canada.

Vi vil takke alle som har bidratt økonomisk og praktisk til prosjektet. Staben ved NINA Forskningsstasjon, Ims, har vært behjelpelig under oppmontering av respirometeret og utførelse av eksperimentene. Prosjektet ble finansiert av Direktoratet for naturforvaltning (DN), Energiforsyningens Fellesorganisasjon (EnFo), Lotek Engineering Inc., Norsk institutt for naturforskning (NINA) og University of Waterloo. Lorraine Fleming har forberedt den engelskspråklige teksten.

Bildene er tatt av Finn Økland og Bengt Finstad, og Svein T. Nilsen har redigert billedmaterialet.

Bengt Finstad  
(Prosjektleder, Norge)

Robert Scott McKinley  
(Projectleder, Canada)

Trondheim, mai 1996

## Preface

This project has been a collaboration between the Norwegian Institute for Nature Research (NINA) and University of Waterloo, Canada. The swim speed chamber used in this experiment was developed and built in Canada.

We would like to thank all contributors to the project. The staff at the NINA Research Station at Ims provided assistance and support during the experiments. Financial support was provided by Directorate for Nature Management (DN), Norwegian Electricity Federation (EnFo), Lotek Engineering Inc., Norwegian Institute for Nature Research (NINA) and University of Waterloo. Lorraine Fleming provided assistance with the English.

The pictures are taken by Finn Økland and Bengt Finstad, and edited by Svein T. Nilsen.

Bengt Finstad  
(Project leader, Norway)

Robert Scott McKinley  
(Project leader, Canada)

Trondheim, May 1996

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# 1 Introduction

Studies of fish behaviour would above all like to have direct measures of the amount and nature of locomotory activity displayed by wild fish. Conventional ultrasonic tags and radio telemetry equipment have been useful in determining positions and movements of individual fish (e.g. Heggberget et al. 1988, Webb et al. 1991, Heggberget et al. 1993, 1995, Økland et al. 1995). These methods ignore movements in depth, horizontal swimming path curvatures and velocity changes over time. Estimated distances swum over time will always be minimum estimates, thus estimates of swimming speed and metabolic costs of activity will also be minimum values (McCleave & Horall 1970, Young et al. 1972). Some biotelemetry systems have been developed to quantify records of physiological events as indices of locomotor activity. Heart rate has been used as a correlate of activity by obtaining ECGs (electrocardiograms) using ultrasonic methods (e.g. Wardle & Kanwisher 1974, Priede & Young 1977) or radio telemetry (e.g. Frank 1968, Weintraub & Mackay 1975). However, heart rate in fish can be affected by stimuli other than exercise (Priede & Young 1977, Priede 1978), and does not necessarily give good correlations with the intensity of physical activity.

A better indicator of fish physical activity seems to be a means of utilizing the fish EMG (electromyogram) (Weatherley et al. 1982, Weatherley & Gill 1987). Telemetry techniques have been developed for the detection of EMGs produced in muscle activity of free swimming fish (Oswald 1978, Luke et al. 1979, Weatherley et al. 1980, Patch et al. 1981, Rogers et al. 1981, Ross et al. 1981, Rogers & Weatherley 1983, Weatherley et al. 1982, Rogers et al. 1984, Kaseloo et al. 1992, McKinley & Power 1992, Booth et al., 1995). EMGs can be used as quantitative indicators of overall fish activity and to obtain quantitative estimates of the metabolic costs of activity.

EMGs are bioelectrical voltage changes that are roughly proportional to the degree and duration of muscle tension (Sullivan et al. 1963). Oxygen demands of muscular activity at any given temperature are rigorously determined by biochemical processes at the tissue level (Weatherley & Gill 1987). It can be assumed that the EMG generated by a representative myomere will be highly correlated with the oxygen consumption that results from the activity of the entire myomere series (Weatherley et al. 1982, Weatherley & Gill 1987). The main swimming muscles in most fish are the axial muscles, which consist of a bilaterally symmetrical series of myomeres (Bone et al. 1978). Thus, EMGs obtained by implanting electrodes in the fish axial muscles can be used as a correlate of activity, and hence of the metabolic costs of activity by calibrating EMGs in terms of oxygen consumption.

## 2 Material and methods

### 2.1 Radio telemetry equipment

EMGs were recorded by use of implantable EMG radio transmitters from Lotek Engineering Inc., Newmarket, Ontario. Dimensions of each transmitter were 5.0 cm long x 1.3 cm in diameter. Transmitter weight in water was 8.5 g (in air 18.4 g), or less than 0.9 % of the body weight of the experimental animal. Such transmitter packages are feasible for fish of approximately 40 cm or more (Kaseloo et al. 1992). The EMG signals emitted from contracting musculature were detected by a pair of flexible teflon coated surgical stainless steel electrodes. An 18 karat gold rod (1 mm diameter and 7 mm long) was attached to each electrode. The rods were bent back onto the electrodes and served to hook and hold the electrodes in the muscle. Signals were processed through an integrator. A radio pulse corresponding to the pulse interval (in milliseconds) was transmitted when a predetermined threshold value of 150  $\mu$ V was reached. Increasing muscle activity (EMG production) thus resulted in a corresponding decrease in the interval between successive radiopulses. The transmitters broadcasted signals within the 142.205-142.430 Mhz range, and transmitter frequencies were spaced 10 kHz apart.

The transmitted EMG interval pulses were detected, measured and stored automatically by a receiver/datalogger (SRX 400 from Lotek Engineering Inc.). Data were downloaded to a computer via an RS-232 serial communication port.

### 2.2 Experimental animals

EMG recording during forced swim trials were carried out on sea ranched salmon released in the River Imsa (south western Norway): 10 Lone stock salmon (6 males and 4 females) and 8 Imsa stock salmon (8 males) (Table 1). Total length of the fish ranged from 49 to 64 cm (Table 1). The fish were caught during return migration in a wolf trap 100 m above the mouth of the River Imsa during the period 27 September-10 October in 1995 (Table 1). EMG transmitters were implanted a few hours to 15 days after catch (Table 1). Between catching and surgery, the fish were kept in dark 4 000 l holding tanks at the NINA Research Station at Ims (southwestern Norway). The forced swim trials were carried out 24-79 hours after surgery (Table 1). Between surgery and experiments, the fish were kept in a dark 700 l holding tank. The water temperatures were in the range 11.0-11.7°C when the experiments were carried out; both in the holding tanks and the swim speed chamber.

Spawning experiments were carried out with 5 sea ranched salmon of the Imsa stock (3 males and 2 females) caught during the period 27 September-31 October, 1995 (Table 1). Total length of the fish ranged from 59 to 69 cm (Table 1). The fish were kept in dark 4000 l holding tanks at the Research Station until EMG transmitters were implanted on 21 November. After one day in a dark 700 l holding tank they were introduced to an indoor spawning tank.

### 2.3 Surgical procedures

The fish were anaesthetized in Metomidate (5 mg l<sup>-1</sup>). Surgery was initiated when operculum rate was slow and irregular. Individual fish were placed on their dorsum in a V shaped surgical table. The gills were flushed with anaesthetic solution during the surgical procedures and with fresh oxygenated water when the surgical procedures were almost finished.

A 3 cm incision was made on the ventral surface posterior to the pelvic girdle using a scalpel. The transmitter was inserted via the incision into the body cavity above the pelvic girdle. To place the antenna, a hollow needle sharpened at one end was inserted into the incision and pushed through the body wall. The antenna wire was threaded into the needle, and the needle was pulled completely through the side of the individual, leaving the antenna wire in place. The two gold rods attached to the electrodes were implanted in the lateral musculature, below the lateral line, with a 21 gauge rod sharpened at one end. The gold rods were placed parallel in the muscle, approximately 5 mm apart, and the gauge rod subsequently removed. The incision was closed using three to five independent silk sutures (2/0 Ethicon). Surgery time was approximately 4-6 min.

### 2.4 Swim speed chamber

EMGs were recorded from Atlantic salmon during forced swim trials in a Blazka-type swim speed chamber/respirometer (described in Booth et al. 1995). The design is based on concentric (coaxial) tubes; the fish chamber is in the inner tube and water returns between the inner and the outer tube. Cross sectional diameter of the tubes is 24 cm and 44 cm, respectively. Total volume of the swim speed chamber is 120 litres. The drive unit is a 3 hp electric motor connected to an impeller. Water velocities are rheostatically controlled. Water velocities within the chamber can be generated up to 2.6 ms<sup>-1</sup> within two seconds (Booth et al. 1995). The edge effect is less than 4 cm at any speed (Booth et al. 1995). During the EMG tests untreated river water was supplied to the chamber via an external pump.

**Table 1.** Atlantic salmon with implanted EMG radio transmitters at the NINA research station at lms in 1995. Fish numbers 1-18 were used in forced swim trials and fish numbers 19-23 were used in spawning experiments.

Fish no.	Stock L = Lone I = lmsa	Sex 1 = male 2 = female	Length (mm)	Weight (gram)	Date of catch	Date of surgery	Date of EMG recording	Time from surgery to forced swim trial (h)
1	L	1	585	1498	27.09	07.10	09.10	48
2	L	1	530	1125	04.10	07.10	10.10	72
3	L	1	574	1547	06.10	08.10	10.10	48
4	L	1	638	2502	09.10	10.10	11.10	24
5	L	1	525	1060	06.10	10.10	11.10	28
6	L	1	549	1265	08.10	17.10		
7	L	2	486	968	04.10	08.10		
8	L	2	530	1256	05.10	08.10	10.10	48
9	L	2	540	1168	10.10	10.10	12.10	41
10	L	2	540	1242	08.10	17.10	19.10	48
11	I	1	594	1466	10.10	12.10	14.10	54
12	I	1	549	1162	28.09	12.10	15.10	79
13	I	1	560	1304	27.09	12.10		
14	I	1	542	1046	10.10	12.10	14.10	47
15	I	1	543	1201	<sup>1</sup>	12.10		
16	I	1	567	1342	06.10	12.10	15.10	70
17	I	1	561	1390	08.10	17.10	18.10	25
18	I	1	554	1229	08.10	17.10	19.10	49
19	I	1	693	2201	10.10			
20	I	1	605	1716	27.09			
21	I	1	588	1472	06.10			
22	I	2	635	2511	31.10			
23	I	2	610	1813	<sup>1</sup>			

<sup>1</sup> The Carlin tag was lost between catch and surgery, the date of catch is therefore unknown.

## 2.5 Forced swim trials, calibration of EMGs to swimming speed

Before recording EMGs, individuals were acclimated for two hours in the swim chamber at a swimming speed of about one fish length per second.

EMGs were first recorded at swimming speed  $0.5 \text{ ms}^{-1}$  (resting speed, about one fish length per second) for five minutes. Then EMGs were recorded at swimming speeds of 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.0, 2.1, 2.2, and  $2.3 \text{ ms}^{-1}$  for two minutes at each speed. Only one fish was recorded at all speeds. The order of speeds in each experiment was a result of how the fish was performing and how we believed we could achieve the best results from individual fish. If a fish was not able to swim for two minutes at a speed, as many EMG pulse intervals as possible at the speed were recorded. Most of the EMG tagged fish were not able to swim at the highest speeds at all. When the fish were not able to swim, they were leaning on the down-

stream screen. EMG pulse intervals recorded when a fish was leaning on the screen and moving back and forth in the swim chamber were removed from the final results.

A black plastic sheet was wrapped around the front of the swim chamber. The fish was stimulated to swim by its desire to keep its head in the dark part of the chamber. Disturbance by people moving in the room was reduced to a minimum.

If a fish was believed to perform well in another series and the results from the first series could be improved, EMGs were recorded in a second series. The fish was allowed to rest between the first and the second series for two hours in the swim chamber at a swimming speed of about one fish length per second.

For each individual there is a survey in Appendix 1 of which swimming speeds EMG recordings were made at, the order of speeds in each series and the number

of EMG pulse intervals that were obtained at each speed.

## 2.6 Spawning experiment

To observe the effects of implanting EMG transmitters just prior to spawning, 3 males and 2 females of the lmsa stock (**Table 1**) were introduced to an artificial indoor spawning tank one day after surgery. In addition the fish were equipped with a Peterson disc tag for visual observation. The tank was 6 m long and 2 m wide, containing a 30 cm deep waterflow over an even distribution of gravel. Four more females with external radio transmitters were kept in the same tank for other experiments.

The fish were observed in the tank during a period of 16 days with a mean of 5.4 observations a day. The duration of the observations averaged 14 minutes, but some observations were just a glance while others lasted for more than an hour.

The EMG signals from these fish were continually received/datalogged; except when data were downloaded to a laptop computer twice a day. The receiver/datalogger was programmed to store an EMG value from each tagged individual approximately every 15th second.

## 3 Results

### 3.1 Surgical procedures

No mortality occurred as a result of surgery, nor could any infection be seen around the incisions. Twelve fish were dissected after the experiments. No evidence of internal damage was seen, except for limited damage to tissue around the transmitter in fish no. 10. In fish no. 10 some abnormal coalescences in the body cavity were cut when the transmitter was inserted.

The gold rods attached to the sensing tips of the electrodes were found 0-15 mm apart in the dissected fish (2-8 mm in all fish, except no. 21 and no. 22), approximately parallel, 0-3 mm from the skin. The red muscle fibers in salmon are situated in a thin layer nearest to the skin, with a thicker layer at the side line. The gold rods were situated at 2 mm above and at 25 mm below the side line in the dissected fish. The gold rods were situated farther from the side line in fish no. 1-13 than in the rest, with a greater chance of touching white muscle fibers. The results, however, do not indicate any differences between the recorded EMG pulse intervals from fish with gold rods close to or distant from the side line.

In fish no. 22 the gold rods had moved within the muscle and were touching each other. The EMG pulse intervals became abnormally short (down to 500-600 ms) the day she started digging in the spawning tank (section 3.3). The low EGM pulse values were probably a result of the gold rods touching each other creating a short circuit. Similar signals were recorded in fish no. 15.

The forced swim trials were carried out between 24 and 79 hours after surgery (**Table 1**). Time from surgery to forced swim trials did not significantly affect the highest possible swimming speed (linear regression analysis,  $r^2 = 0.10$ ,  $P = 0.27$ ). Time from surgery to forced swim trials did not significantly affect the standard deviations of the individual EMGs in each series (linear regression analyses (one for each swimming speed),  $r^2$  values from  $< 0.001$  to 0.40,  $P$  values from 0.25 to 0.96; only the standard deviation from the first recording in individual fish at the swimming speed in question was included in the regression).

Dissection of the fish in the spawning experiment (section 3.3) revealed that the dominant male seemed fully capable of spawning with an implanted EMG transmitter. One of the females had also spawned, while the transmitter in the other female inhibited spawning.

## 3.2 Forced swim trials, calibration of EMGs to swimming speed

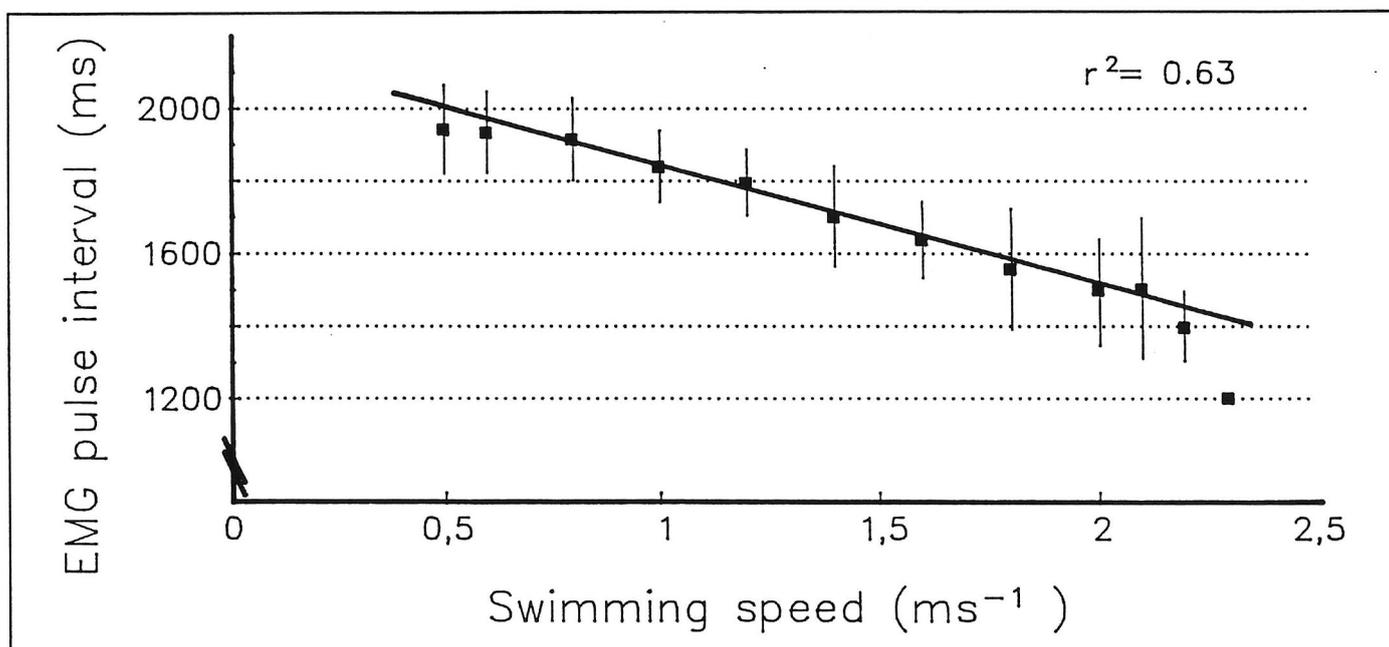
In the forced swim trials EMGs were not recorded from fish no. 6, 7, 13 and 15 (Table 1). The signals from the transmitter in fish no. 6 suddenly disappeared (end of battery life). The transmitter in fish no. 7 and 13 suffered from an unknown technical failure. (The same transmitter was used in both fish to see if the failure was due to an incorrect implantation). In fish no. 15 the gold rods probably touched each other (section 3.1).

During the forced swim trials most fish were swimming in a relatively consistent fashion at the lowest speeds. When the speed was increased against the individual speed of fatigue, the fish became gradually more uneasy, varied the position in the swim chamber and accelerated irregularly. At high swimming speeds burst and glide swimming was observed in several fish: one or two rapid undulatory bursts followed by gliding forward while the body was held straight.

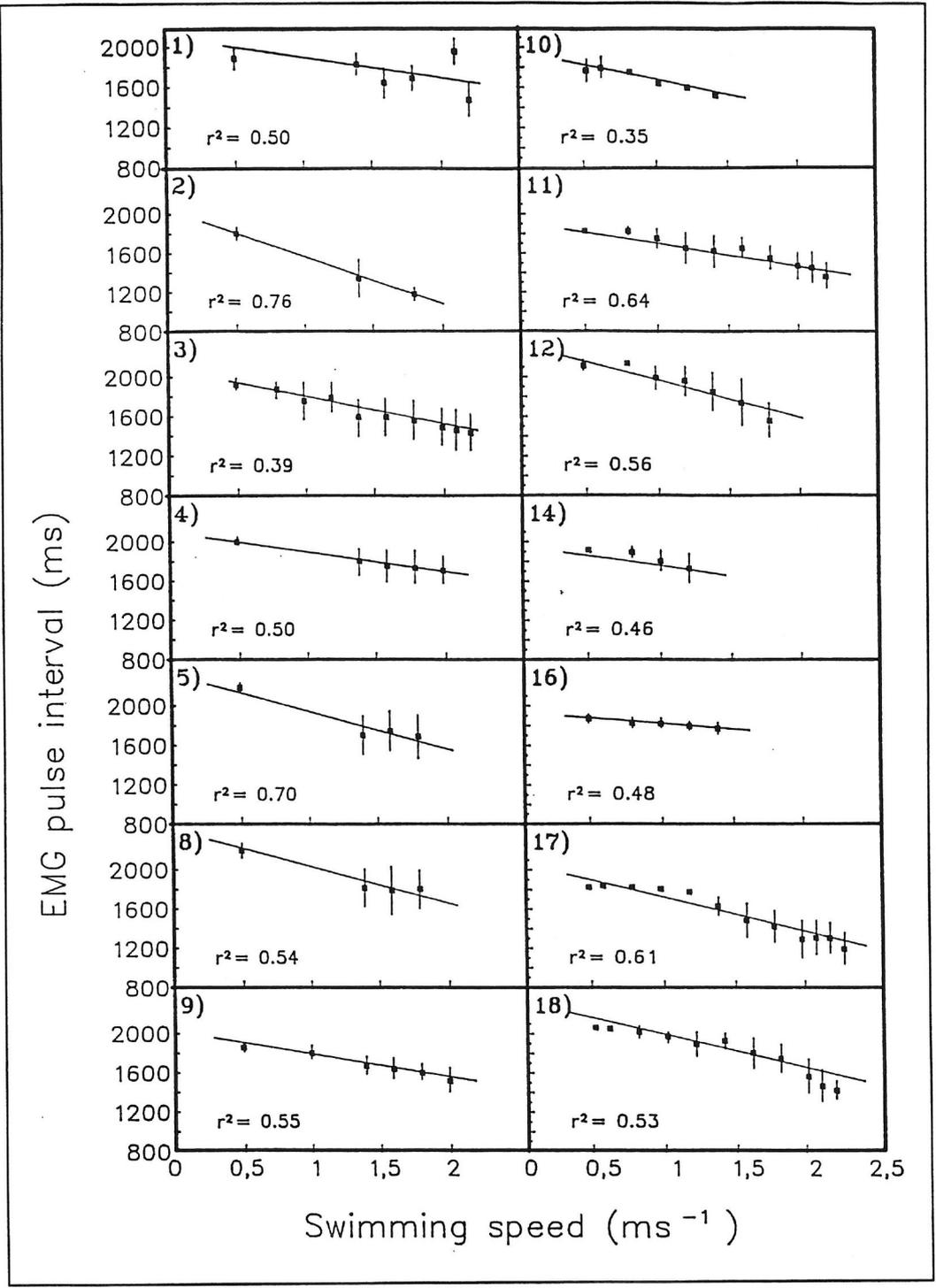
A linear regression describes the relationship between forced swimming speed and average EMG pulse intervals when recordings at each swimming speed in all individuals were included ( $r^2 = 0.63$ ,  $P < 0.001$ ) (Figure 1). A power curve describes the relationship slightly better ( $r^2 = 0.64$ ). Individual fish differ in EMGs recorded at resting speed ( $0.5 \text{ ms}^{-1}$ ) (Figure 2), and thus, a higher correlation between swimming speed and EMG pulse intervals was obtained when the differences in resting EMG levels were adjusted for: EMG pulse intervals in individual fish were divided by the EMG average obtained at resting speed in the same series as they were recorded ( $r^2 = 0.75$ ,  $P < 0.001$ ) (Figure 3).

### 3.2.1 Variation within individuals

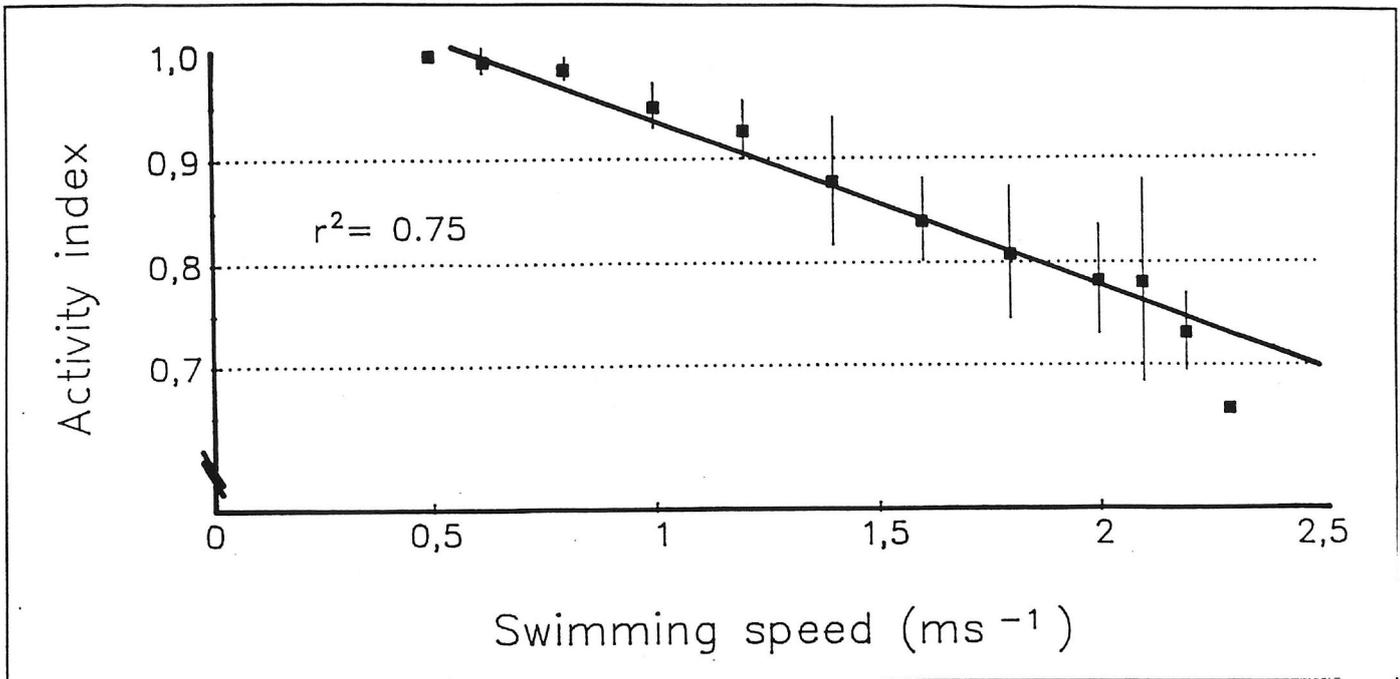
In some cases EMG pulse intervals recorded at a swimming speed varied within individuals when recordings at the speed were repeated within a series. Similar variations occurred when EMGs were recorded at certain swimming speeds in both the first and the second series:



**Figure 1.** Calibration of EMG pulse intervals to swimming speed in Atlantic salmon by use of implanted EMG radio transmitters. The markers (with standard deviations) represent EMG averages of individual average values obtained at each swimming speed in each series<sup>1</sup>. Salmon of both the lmsa ( $n = 6$ ) and the Lone stock ( $n = 8$ ) are represented in the figure. (Decreased EMG pulse intervals indicates increased muscle activity.). <sup>1</sup>Series is defined in «2.5 Forced swim trials, calibration of EMGs to swimming speed» and Appendix 1.



**Figure 2.** Calibration of EMG pulse intervals to swimming speed in individual Atlantic salmon by use of implanted EMG radio transmitters. The markers (with standard deviations) represent an EMG average at each swimming speed. (Decreased EMG pulse intervals indicate increased muscle activity.)



**Figure 3.** Calibration of activity index to swimming speed in Atlantic salmon by use of implanted EMG radio transmitters. The activity index is obtained by dividing EMG pulse intervals in individual fish by the EMG average at resting speeds in the same series<sup>1</sup> as they were recorded. Salmon of both the lmsa ( $n = 6$ ) and the Lone stock ( $n = 8$ ) are represented in the figure. The lines gives the standard deviations. (Decreased activity index indicates increased muscle activity.). <sup>1</sup>Series is defined in «2.5 Forced swim trials, calibration of EMGs to swimming speed» and Appendix 1.

Certain swimming speeds were repeated more than once within a series (**Appendix 1**). In 3 cases the EMG pulse intervals were significantly longer when repeated (Mann-Whitney U tests, P-values < 0.005), in 5 cases significantly shorter (Mann-Whitney U tests, P-values < 0.05) and in 8 cases no significant differences were found (Mann-Whitney U tests, P-values > 0.05).

In 8 fish EMGs were recorded at resting speed in both the first and the second series (**Appendix 1**). In one fish the EMG pulse intervals were significantly longer in the second series (Mann-Whitney U test,  $P < 0.001$ ), and in four fish the EMG values were significantly shorter (Mann-Whitney U tests, P-values < 0.001).

Certain swimming speeds were recorded in both the first and the second series (Appendix 1). In 6 cases the EMG pulse intervals were significantly longer in the second series (Mann-Whitney U tests, P-values < 0.009), in 2 cases the EMG pulse intervals were significantly shorter (Mann-Whitney U tests, P-values < 0.05) and in 9 cases no significant differences were found (Mann-Whitney U test, P-values > 0.05).

### 3.2.2 Variation between individuals

Linear regressions describe the effect of swimming speed on EMG pulse intervals in individual fish ( $r^2$  from 0.35 to 0.76) (**Figure 2**). EMGs recorded at resting speed ( $0.5 \text{ ms}^{-1}$ ) differ between individuals. The linear regression slopes also differ between individuals ( $\beta$  from -514 to -112). All regression slopes significantly differ from zero (P values < 0.001).

### 3.2.3 Variation between stocks

The linear regressions that describe the effect of swimming speed on average EMG pulse intervals in fish of the lmsa stock and fish of the Lone stock are significantly different ( $P < 0.05$ ) (**Figure 4**). (Regression equation of lmsa salmon:  $y = -378x + 2200$ ,  $r^2 = 0.77$ , 95 % confidence interval of the slope is  $-378 \pm 47$ . Regression equation of Lone salmon:  $y = -225x + 2027$ ,  $r^2 = 0.45$ , 95 % confidence interval of the slope is  $-225 \pm 66$ .)

### 3.3 Spawning experiment

All five fish were immediately swimming around and seemed to be in a good condition when they were introduced to the spawning tank. The males began fighting the same day.

Male no. 19 appeared as the dominant male from the first day in the spawning tank. In the 16 days the experiment lasted he was always active, always together with the most active female(s) and always aggressive towards the other males if they were trying to swim around in the tank. Altogether 50 quivers were

observed and he was observed quivering close to all the females in the tank. Dissection after the experiment was finished showed that he had probably spawned several times. The EMG transmitter stopped transmitting signals on the eighth day of the experiment because the battery power had ended

Male no. 20 was observed quivering close to two females, but was mostly chased away by male no. 19. He jumped out of the tank and died after four days.

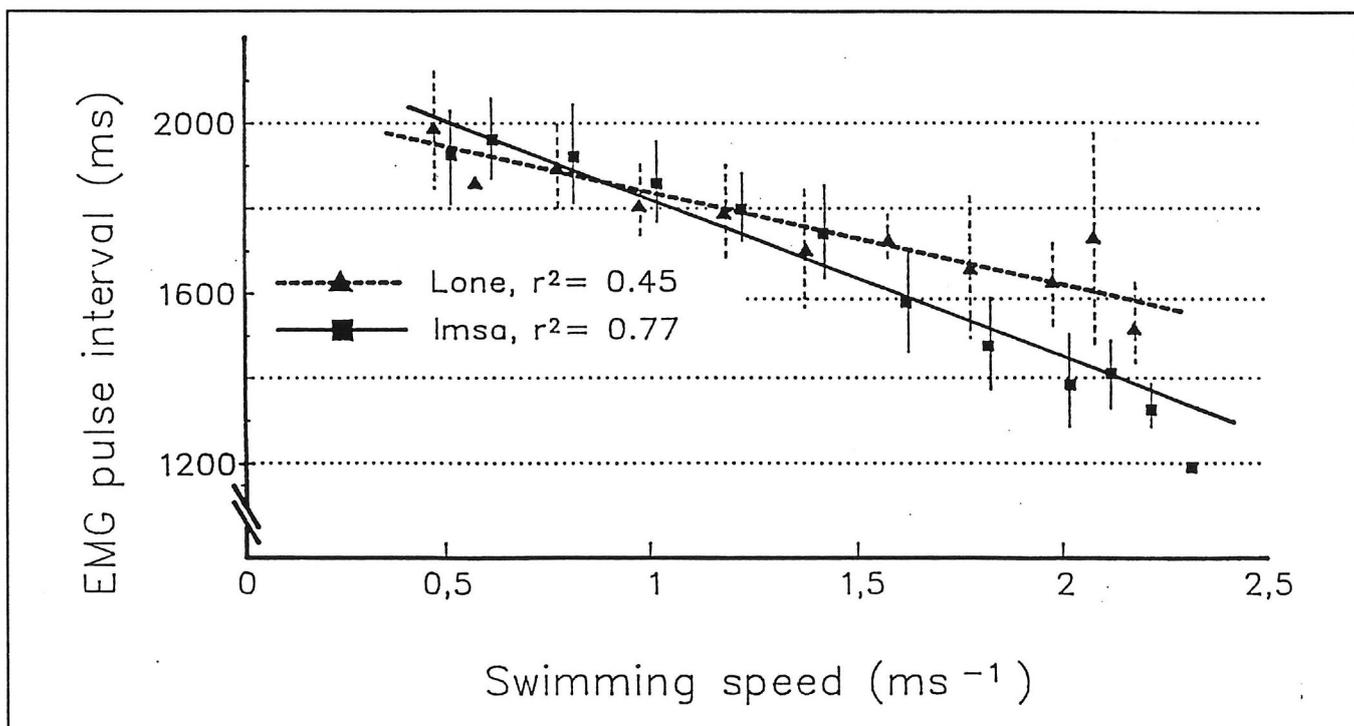
Male no. 21 lay on the bottom in a corner most of the time. He tried to swim around in the tank a few times, but was immediately chased back by male no. 19. Except for being dominated to the point of inactivity by

no. 19, he seemed to be in a good condition.

Female no. 22 had a relatively high level of activity from the first day in the tank. She was observed digging a pit 7 days after introduction to the tank and another pit the day after. Altogether 61 cuttings were observed. Male no. 19 was quivering close to her when she was digging. It is possible that she made more nest pits than the two observed. She was killed 9 days after introduction to allow other females to spawn. Dissection revealed that she had spawned, and that she had eggs for one or two spawnings left. Unfortunately, EMGs recorded during the spawnings were useless, because the gold tips had moved in the muscle and were touching each other (section 3.1).

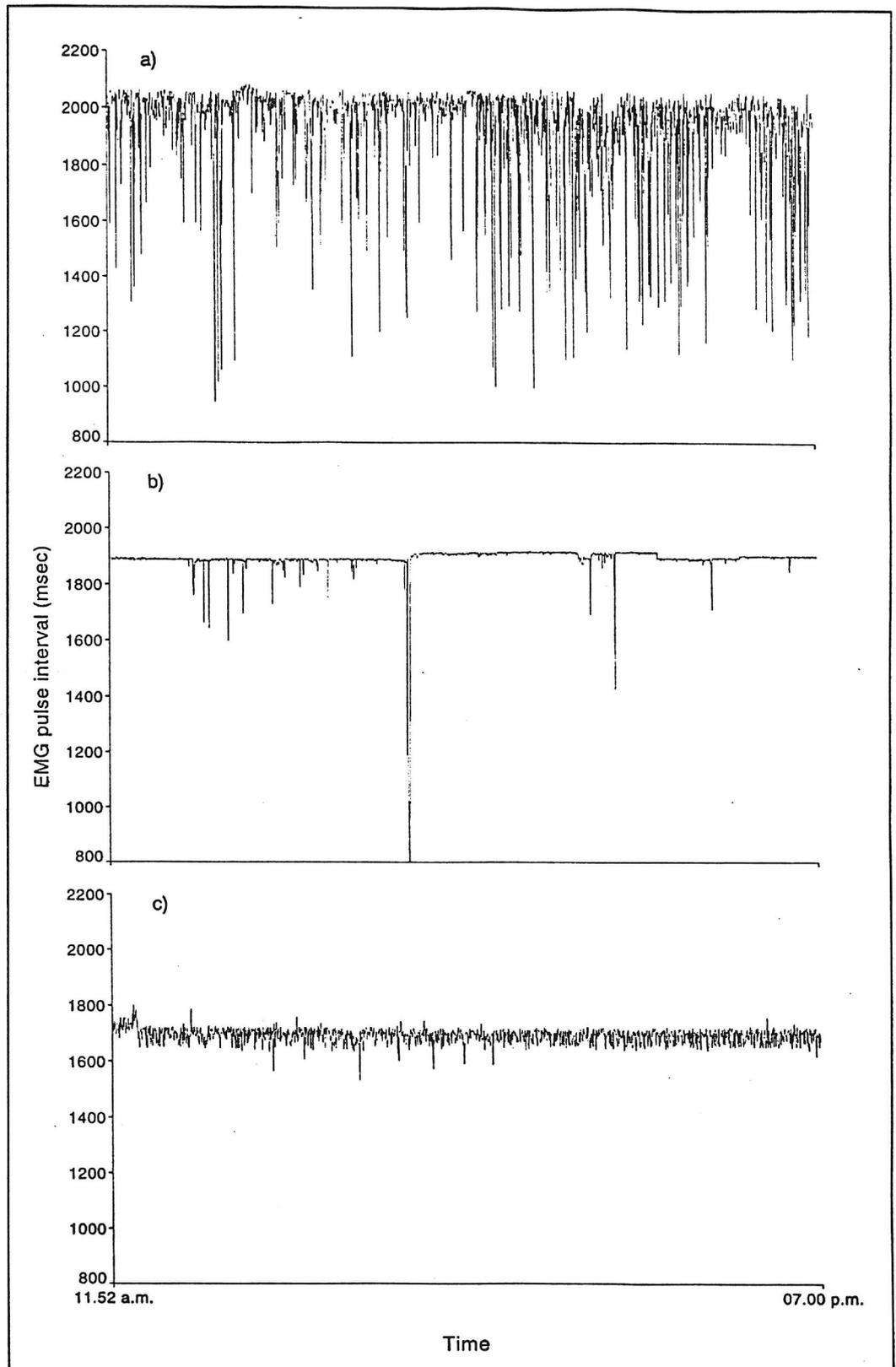
Female no. 23 was active the 7 first days in the tank, without digging. The first day after introduction to the tank she was observed in another female's nest pit. The activity level decreased in second half of the experiment, but she was often seen swimming along the edges of the tank. When the experiment was finished it was impossible to strip her. Dissection revealed that the EMG transmitter had inhibited spawning.

Continually EMG recordings from the fish in the spawning tank differed when the fish were involved in different activities (Figure 5).



**Figure 4.** Calibration of EMG pulse intervals to swimming speed in Atlantic salmon by use of implanted EMG radio transmitters. The markers (with standard deviations) represent EMG averages of individual average values obtained at each swimming speed in each series<sup>1</sup>. The slopes of the linear regressions are significantly different ( $P < 0.05$ ) between the lmsa stock ( $n = 6$ ) and Lone stock ( $n = 8$ ). (Decreased EMG pulse intervals indicate increased muscle activity.). <sup>1</sup>Series is defined in «2.5 Forced swim trials, calibration of EMGs to swimming speed» and Appendix 1.

**Figure 5.** Continually EMG recordings from three Atlantic salmon with implanted EMG radio transmitters in a spawning tank. (Decreased EMG pulse intervals means increased muscle activity.) An EMG value was received/data-logged about every 15th second from each fish. The EMGs were recorded from 11.52 a.m. to 07.00 p.m. on 2 of October in 1995. The fish were visually observed in altogether 150 minutes during this period. During the visual observations. Male no. 19 (a) was courting female no. 22 and a female with an external radio transmitter. He was observed quivering 36 times. Male no. 21 (b) was laying on the bottom almost without moving. Female no. 23 (c) did not take part in any spawning activity. She had quiet swimming movements above the bottom without moving much around in the tank.



## 4 Discussion

### 4.1 Surgical procedures

The surgical procedures used in this study worked out satisfactory. No mortality occurred as a result of surgery and no infections were observed. The fish recovered soon after surgery, and no fish displayed balance or swimming problems.

The forced swim trials were carried out between 24 and 79 hours after surgery. Time from surgery to forced swim trials did not significantly affect the highest speed at which individuals were able to swim. The best performing fish was swimming a forced trial in the swim chamber only 25 hours after surgery. However, some of the fish may have performed better if they were allowed to rest for a longer period before the forced swim trials. Also the long term effects of exercise soon after surgery are unknown, which is important if the fish are going to be released for field experiments after the forced swim trials. Kaseloo et al. (1992) reported that following initial implantation there was a period, usually less than two days, during which some greater variation in pulse intervals was seen. They presumed that this variability resulted from initial physical trauma to the muscle at the electrode implantation site. In this study, we did not find that time from surgery to forced swim trials affected the variation in pulse intervals.

The two gold rods attached to the sensing tips of the electrodes were situated in the muscle approximately 5 mm apart. In two fish the gold rods had moved in the muscle and were touching each other. This resulted in a characteristic short and useless EMG pulse intervals. One of the fish with touching gold rods was a female in the spawning experiment. The rods probably connected the day she began digging. Therefore, vigorous body movements such as digging may move the electrodes and gold rods in the muscle. At least in field experiments using implanted EMG transmitters, it would be an advantage to increase the distance between the sensing tips. The effects on EMG pulse intervals from situating the sensing tips at different distances are unknown and should be investigated further.

The spawning experiment showed that salmon are able to spawn with internal EMG transmitters, but that the transmitter may inhibit spawning. One of the males and one of the females in the experiment had spawned, but in one female spawning was completely inhibited by the transmitter.

### 4.2 Forced swim trials, calibration of EMGs to swimming speed.

We were able to calibrate EMG pulse intervals from axial red musculature to swimming speed in a swim speed chamber.

Linear regression analyses showed that the relationship between forced swim speed and EMG pulse intervals in individual fish remained fairly highly correlated ( $r^2$  from 0.35 to 0.76). However, in some cases EMG pulse intervals recorded at a swimming speed varied within individuals when recordings at the speed were repeated within a series. Similar variations occurred when EMGs were recorded at certain swimming speeds in both the first and the second series. The variation in EMGs within individuals is probably explained by different behaviours in the respirometer. At the lowest speeds most fish were swimming in a relatively consistent fashion. When the speed was increased against the individual speed of fatigue, the fish became gradually more uneasy, varied the position in the swim chamber and accelerated irregularly. Burst and glide swimming were observed in several fish at high speeds. Representative recordings from each individual are most important if conclusions concerning one individual in field experiments are drawn from EMGs recorded from the same individual in laboratory swim trials.

Most teleost fish have discrete red and white (mosaic) muscle groups which represent separate low and high speed muscle systems (Bone 1978, Johnston 1981). Rome et al. (1992) found that the intensity of red muscle activity increased with speed until a maximal level was attained and then was maintained with further increases in speed. In contrast, Jayne & Lauder (1994) found that at high speeds of burst and glide swimming the intensity of red muscle activity decreased, while the intensity of white muscle activity increased. The EMG recordings from red musculature in our study covered all swimming speeds, from sustained swimming, burst and glide swimming, until fatigue. In some individuals the EMG pulse interval averages remained high at the lowest speeds and then decreased in a curvilinear fashion at higher speeds (decreasing EMG pulse intervals means increasing muscle activity). In other individuals the relationship between swimming speed and EMG averages were linear. However, in all fish the EMG pulse intervals recorded in the red musculature decreased with increasing swimming speeds, until fatigue. This might support the findings of Rome et al (1992). Another explanation is the fact that implanted electrodes in the red muscle can detect the operation of both the red and the white muscle groups (Ross et al. 1981, Sisson & Sidell 1987, McKinley & Power 1992). Until more is known about how fish use slow and fast muscle fibers, and to what extent electrodes in red

muscle detects activity in white muscle, it is difficult to suggest an expected shape of the relationship between swimming speed and EMG pulse intervals in individual fish. Salmonids are able to maintain a position against a current using their large pectoral fins as depressors, which is usually effective only at the lower velocities (Kutty & Saunders 1973). This behaviour may also affect the shape of the relationship between swimming speed and EMG pulse intervals in individual fish.

EMGs recorded at resting speed ( $0.5 \text{ ms}^{-1}$ ) differed between individuals, and the regression slopes differed between individuals. The variation in EMGs between individuals may be due to individual differences in behaviour and/or physiology. The variation may also be due to different situations of the sensing electrodes in the muscles. The effects of small variations in distance between the electrodes, and the effects of situating the electrodes in different parts of the red musculature are unknown. In 13 fish in this study the sensing electrodes were probably situated farther from the side line than in the rest of the fish with a greater chance of touching white musculature. However, we could not find any differences in recorded EMGs.

When all the average EMGs from all individuals were combined, a power curve described the relationship between EMG pulse intervals and swimming speed ( $r^2 = 0.64$ ) slightly better than a linear regression ( $r^2 = 0.63$ ). Kaseloo et al. (1992) and McKinley & Power (1992) found similar linear relationships between forced swim speed and EMG in rainbow trout (*Oncorhynchus mykiss*) and lake sturgeon (*Acipenser fulvescens*) respectively. Since individual fish in this study varied in their EMG resting levels a higher correlation between swimming speed and EMG pulse intervals was obtained when the differences in resting levels were adjusted for ( $r^2 = 0.75$ ).

Salmon stocks may differ in the linear relationship between EMG pulse intervals and swimming speed. We recorded EMGs from sea ranched salmon of two different stocks and found significant differences between the stocks in the regression slopes. However, definitive conclusions should not be drawn from this. When sample sizes are less than ten, inference is an unexplored area of mathematical statistics (Seaman & Jaeger 1990). In this study EMGs were recorded from six and eight individuals of each stock. Thus, possible differences between salmon from different stocks should be further investigated with greater samples and fish from several stocks. The observed differences between the stocks may be due to different behaviour in the swim chamber. This aspect should be included in future studies of the behaviour of salmon in a swim speed chamber.

### 4.3 Spawning experiment

The implanted EMG transmitter did not seem to greatly affect spawning behaviour in five fish in a spawning tank. The fish were introduced to the tank one day after surgery, and the males were already fighting the same day. The largest male completely dominated the other males. Despite the implanted transmitter, he had probably spawned several times. One female spawned several times, but in another female the transmitter inhibited spawning completely. This may have prevented this female from initiating normal spawning behaviour.

The electromyograms obtained by continuous data-logging showed that it is possible to use EMG transmitters as quantitative indicators of overall fish activity. To some extent behaviours can also be inferred from such recordings. It seems possible to recognise different activities (like swimming, spawning, digging, inactiveness) by analysing EMG recordings when more electromyograms from controlled laboratory experiments are collected. Thus, it seems possible to determine the onset of spawning in individual fish in field experiments. The activity level may also indicate the dominance position of individual males, which in some studies is important (e.g. studies concerning the spawning behaviour of farmed salmon compared to wild salmon).

An EMG value was received/datalogged about every 15th second from each fish, which resulted in a huge amount of data and a need for downloading the data twice a day. Averaging EMG over shorter or longer periods is possible, but averaging of relatively large periods will limit the detail of the analysis.

### 4.4 The use of EMG transmitters in field experiments, conclusion.

The use of EMG radio transmitters in field experiments seems promising. It is possible to indicate overall fish activity quantitatively. It also seems possible to recognise different activities and determine the onset of spawning in individual fish.

The calibration of EMG pulse intervals to swimming speed resulted in high correlations, especially when EMG averages from several fish were included and individual differences in EMG resting levels were adjusted for. Higher correlations than we obtained in individual fish are probably achievable if EMGs are recorded for a longer period at each speed and swim trials are repeated. Thus, it is possible to calibrate EMG pulse intervals to swimming speeds in individual fish before they are released in field experiments, and

it is possible to use a calibration with fish from the same stock to draw conclusions in field experiments. Since regression slopes differed between individuals, the inaccuracy will be least when the calibration is made for individual fish before release. In some field experiments this procedure may not be desirable. If differences in regression slopes between individuals are caused by differences in implantation of the electrodes, correlation of the calibration including several fish may be easily increased. Thus, the effects of electrode situation in the muscle on EMG pulse intervals should be further investigated. The possible differences between stocks should also be further investigated to analyse the effectiveness of using a calibration including fish from different stocks.

Several studies have calibrated oxygen consumption to swimming speed (e.g. Brett 1964, Brett & Sutherland 1965). Successful calibration of EMG pulse intervals to swimming speed opens the possibility to calibrate EMG to oxygen consumption. Weatherley, et al. (1982) and McKinley & Power (1992) calibrated EMGs to oxygen consumption in rainbow trout and lake sturgeon, respectively. Weatherley et al. (1982) found regression slopes differed in the relationship between EMG and oxygen consumption when the fish were swimming in a forced swim chamber compared to a spontaneous activity chamber. The shift from one regression to the other occurred on a precise EMG pulse interval. These findings makes the use of EMGs as estimators of the metabolic costs of activity in field experiments more complicated, but opens a possibility to decide whether a fish is cruising or having more desultory movements.

## 5 References

- Bone, Q. 1978. Locomotor muscle. - Pp. 361-424. in Hoar, W. S. & Randall, D. K., eds. Fish physiology,
- Booth, R.K., McKinley, R.S., Økland, F. & Sisak, M.M. 1995. *In situ* measurement of swimming performance in wild Atlantic salmon (*Salmo salar*), using radio transmitted electromyogram (EMG) signals. Manuscript.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. - J. Fish. Res. Bd. Canada 21: 1183-1226.
- Brett, J.R. & Sutherland, D.B. 1965. Respiratory metabolism of pumpkinseed (*Lepomis gibbosus*) in relation to swimming speed. - J. Fish. Res. Bd. Canada 22: 405-409.
- Frank, T.H. 1968. Telemetering the electrocardiogram of free swimming *Salmo irideus*. - IEEE Trans. Biomed. Eng. 15: 111-114.
- Heggberget, T.G., Hansen, L.P. & Næsje, T.F. 1988. Within-river spawning migration of Atlantic salmon (*Salmo salar*). - Can. J. Fish. Aquat. Sci. 45: 1691-1698.
- Heggberget, T.G., Økland, F. & Ugedal, O. 1993. Distribution and migratory behaviour of adult wild and farmed Atlantic salmon (*Salmo salar*) during return migration. - Aquaculture 118: 73-83.
- Heggberget, T.G., Økland, F. & Ugedal, O. 1995. Prespawning migratory behaviour of wild and farmed Atlantic salmon (*Salmo salar*) in a North Norwegian river. - Aquacult. Fish. Manage. Accepted manuscript, 19 pp.
- Jayne, B.C. & Lauder, G.V. 1994. How swimming fish use slow and fast muscle fibers: implications for models of vertebrate muscle recruitment. - J. Comp. Physiol. A, 175: 123-131.
- Johnston, I.A. 1981. Structure and function of fish muscles. - Symp. zool. Soc. Lond. 48: 71-113.
- Kaseloo, P.A., Weatherley, A.H., Lotimer, J. & Farina, M.D. 1992. A biotelemetry system recording fish activity. - J. Fish Biol. 40: 165-179.
- Kutty, M.N. & Saunders, R.L. 1973. Swimming performance of young Atlantic salmon (*Salmo salar*) as affected by reduced ambient oxygen concentration. - J. Fish. Res. Board. Can. 30: 223-227.
- Luke, D.M., Pincock, D.G., Sayre, P.D. & Weatherley, A.H. 1979. A system for the telemetry of activity-related information from free swimming fish. - Proc. 2nd Int. Conf. Wildl. Biotelemetry, pp. 77-85. University of Wyoming, Laramie.
- McCleave, J.D. & Horrall, R.M. 1970. Ultrasonic tracking of homing cutthroat trout (*Salmo clarki*) in Yellowstone lake. - J. Fish. Res. Bd. Canada 27: 715-730.

- McKinley, R.S. & Power, G. 1992. Measurement of activity and oxygen consumption for adult lake sturgeon (*Acipenser fluvescens*) in the wild using radio-transmitted EMG signals. - Pp. 307-318 in Priede, I.G. & Swift, S.M., eds. *Wildlife telemetry: Remote sensing and tracking of animals*.
- Oswald, R.L. 1978. The use of telemetry to study light synchronization with feeding and gill ventilation rates in *Salmo trutta*. - *J. Fish Biol.* 13: 729-739.
- Patch, J.R., Pincock, D.G., Weatherley, A.H. & Rogers, S.C. 1981. A field system for telemetry of fish energetics. - *Proc. 3rd Int. Conf. Wildl. Biotelemetry*, pp. 129-140. University of Wyoming, Laramie.
- Priede, I.G. 1978. Behavioural and physiological rhythms of fish in their natural environment, as indicated by ultrasonic telemetry of heart rate. - Pp 153-168. in Thorpe, J. E., ed. *Rhythmic activity of fishes*.
- Priede, I.G. & Young, A.H. 1977. The ultrasonic telemetry of cardiac rhythms of wild brown trout (*Salmo trutta* L.) as an indicator of bio-energetics and behaviour. - *J. Fish Biol.* 10: 299-318.
- Rogers, S.C. & Weatherley, A. H. 1983. The use of opercular muscle electromyograms as an indicator of the metabolic costs of fish activity in rainbow trout, *Salmo gairdneri* Richardson, as determined by radiotelemetry. - *J. Fish Biol.* 23: 535-547.
- Rogers, S.C., Church, D.W., Weatherley, A.H. & Pincock, D.G. 1984. An automated ultrasonic telemetry system for the assessment of locomotor activity in free-ranging rainbow trout, *Salmo gairdneri*, Richardson. - *J. Fish Biol.* 25: 697-710.
- Rogers, S.C., Weatherley, A.H., Pincock, D.G. & Patch J.R. 1981. Telemetry, electromyograms, and oxygen demands of fish activity. - *Proc. 3rd Int. Conf. Wildl. Biotelemetry*, pp. 141-150. University of Wyoming, Laramie.
- Rome, L.C., Choi, I.-H., Lutz, G. & Sosnicki, A. 1992. The influence of temperature on muscle function in the fast swimming scup I. Shortening velocity and muscle recruitment during swimming. - *J. Exp. Biol.* 163: 259-279.
- Ross, L.G., Watts, W. & Young, A.H. 1981. An ultrasonic biotelemetry system for the continuous monitoring of tail-beat rate from free-swimming fish. - *J. Fish Biol.* 18: 479-490.
- Seaman, J.W. & Jaeger, R.G. 1990. *Statisticae dogmaticae: a critical essay on statistical practise in ecology*. - *Herpetologica* 46: 337-346.
- Sisson, J.E. & Sidell, B.D. 1987. Effect of thermal acclimation on muscle fiber recruitment of swimming striped bass (*Morone saxatilis*). - *Physiol. Zool.* 60: 310-320.
- Sullivan, G.H., Hoefener, C. & Bolie, V.W. 1963. Electronic systems for biological telemetry. - Pp. 83-106 in Slater, L.E., ed. *Bio-telemetry: the use of telemetry in animal behaviour and physiology in relation to ecological problems*.
- Wardle, C.S. & Kanwisher, J.W. 1974. The significance of heart rate in free swimming cod, *Gadus morhua*: some observations with ultra-sonic tags. - *Mar. Behav. Physiol.* 2: 311-324.
- Weatherley, A.H. & Gill, H.S. 1987. *The biology of fish growth*. Academic Press, London.
- Weatherley, A.H., Rogers, S.C. & Pincock, D.G. 1980. Use of telemetry in monitoring intensity and energetics of activity in free-swimming fish with reference to zinc pollution. - *Can. Tech. Rep. Fish. Aquat. Sci.* 975: 162-170.
- Weatherley, A.H., Rogers, S.C., Pincock, D.G. & Patch, J.R. 1982. Oxygen consumption of active rainbow trout, *Salmo gairdneri* Richardson, derived from electromyograms obtained by radiotelemetry. - *J. Fish Biol.* 20: 479-489.
- Webb, J.H., Hay, D.W., Cunningham, P.D. & Youngson, A.F. 1991. The spawning behaviour of escaped farmed and wild adult Atlantic salmon (*Salmo salar* L.) in a northern Scottish river. - *Aquaculture* 98: 97-110.
- Weintraub, M.J. & Mackay, R.S. 1975. Respiratory and heartbeat synchrony studied by telemetry in the trout (*Salmo gairdneri*). - *Copeia* 1: 78-85.
- Young, A.H., Tytler, P., Holliday, F.G.T. & MacFarlane, A. 1972. A small sonic tag for measurement of locomotor behaviour in fish. - *J. Fish Biol.* 4: 57-65.
- Økland, F., Heggberget, T.G. & Jonsson, B. 1995. Migratory behaviour of wild and farmed Atlantic salmon (*Salmo salar*) during spawning. - *J. Fish Biol.* 46: 1-7.

**Appendix 1. Forced swim trials in a swim speed chamber with EMG radio transmitter tagged Atlantic salmon in 1995. A survey of swimming speeds, number of EMG recordings for individual fish and the order of speeds in each series are presented. Number of EMG pulse intervals obtained at each speed is given in parentheses.**

**Fish no. 1:**

1st series 1.4 (55) 1.6 (78) 1.8 (83)  
 2nd series 2.1 (66) 2.2 (48) 0.5 (189)

**Fish no. 2:**

1st series 0.5 (225) 1.4 (103)  
 2nd series 0.5 (32) 1.8 (4)

**Fish no. 3:**

1st series 0.5 (158) 1.4 (96) 1.6 (94) 1.8 (92) 2.0 (61) 2.1 (39) 2.2 (18) 1.4 (45) 2.2 (18)  
 1.4 (45) 2.2 (7)  
 2nd series 0.8 (54) 1.0 (59) 1.2 (63) 1.4 (58) 1.6 (61) 1.8 (64) 2.0 (66) 2.1 (6)

**Fish no. 4:**

1st series 0.5 (142) 1.4 (49) 1.6 (56) 1.8 (65) 2.0 (30)

**Fish no. 5:**

1st series 0.5 (135) 1.4 (61) 1.6 (46) 1.8 (17)  
 2nd series 0.5 (46) 1.8 (40)

**Fish no. 8:**

1st series 0.5 (105) 1.4 (67) 1.6 (50) 1.8 (44)

**Fish no. 9:**

1st series 0.5 (128) 1.4 (85) 1.6 (72) 1.8 (67) 2.0 (51) 1.0 (53) 1.2 (68) 1.4 (56) 1.6 (64)  
 1.8 (68) 2.0 (55)

**Fish no. 10:**

1st series 0.5 (166) 0.6 (97) 0.8 (73) 1.0 (79) 1.2 (85) 1.4 (22)

**Fish no. 11:**

1st series 0.5 (105) 0.8 (70) 1.0 (71) 1.2 (73) 1.4 (56) 1.6 (73) 1.8 (63) 2.0 (64) 2.1 (16)  
 2nd series 0.5 (205) 1.8 (80) 2.0 (60) 2.1 (67) 2.2 (25)

**Fish no. 12:**

1st series 0.5 (133) 0.8 (55) 1.0 (63) 1.2 (63) 1.4 (63) 1.6 (44)  
 2nd series 0.5 (147) 1.6 (70) 1.8 (48)

**Fish no. 14:**

1st series 0.5 (151) 0.8 (61) 1.0 (62) 1.2 (51)  
 2nd series 0.5 (121) 1.2 (70)

**Fish no. 16:**

1st series 0.5 (145) 0.8 (65) 1.0 (63) 1.2 (68)  
 2nd series 0.5 (161) 1.2 (69) 1.4 (86)

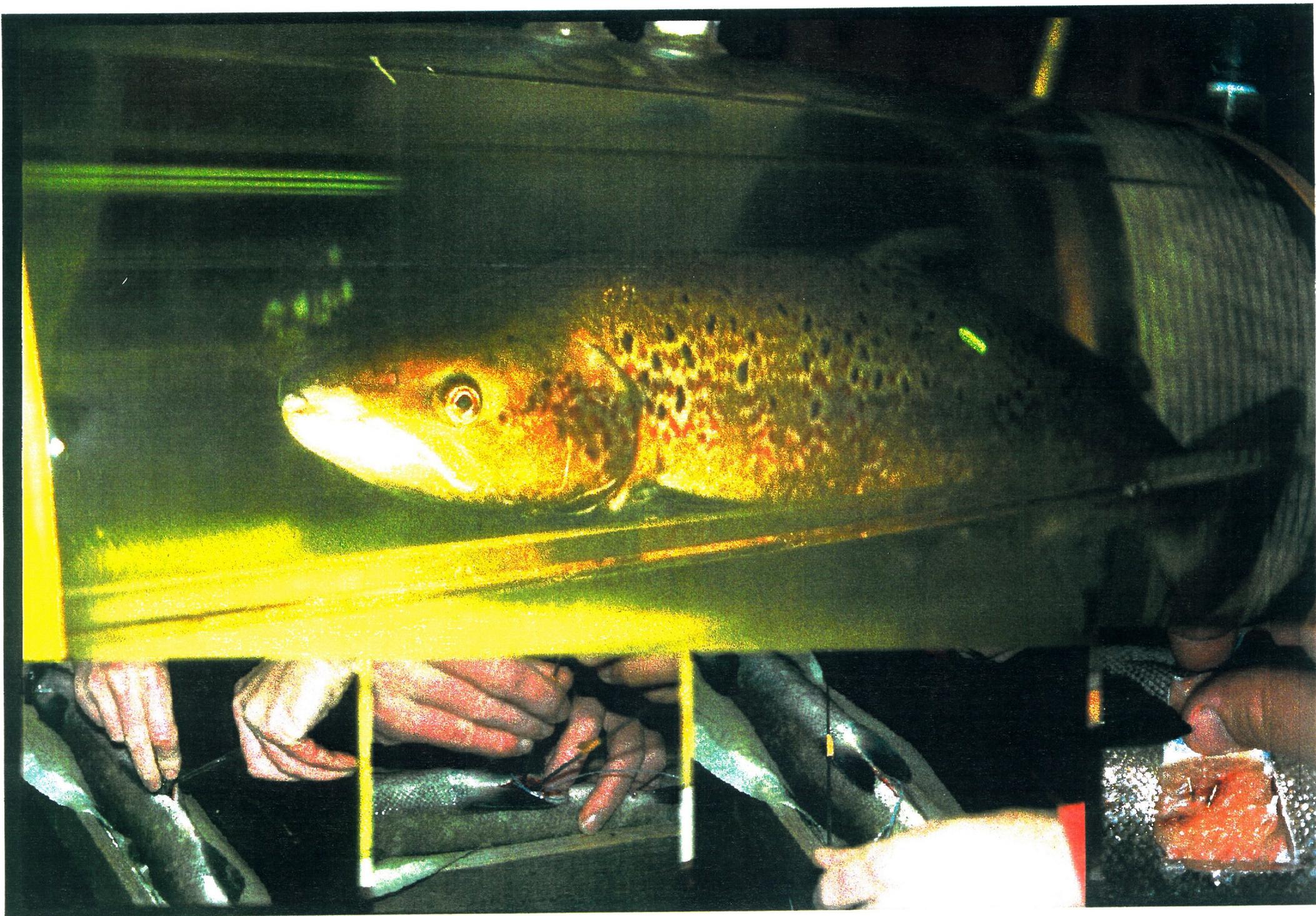
**Fish no. 17:**

1st series 0.5 (174) 1.4 (102) 1.6 (86) 1.8 (30) 0.8 (75) 1.0 (69) 1.2 (70) 1.4 (70) 1.6 (24)  
 1.8 (50) 2.0 (27) 2.1 (31) 2.2 (21) 2.3 (28) 1.8 (86) 1.6 (29) 2.0 (16)  
 2nd series 0.5 (83) 0.6 (65) 1.4 (74) 1.6 (40) 1.8 (9) 2.1 (19) 1.8 (18) 2.2 (8)

**Fish no. 18:**

1st series 0.5 (144) 0.6 (64) 0.8 (61) 1.0 (66) 1.2 (67) 1.4 (67) 1.6 (75) 1.8 (73) 2.0 (38)  
 2.1 (12) 0.6 (67) 0.8 (62) 1.0 (62) 1.2 (62) 1.4 (67) 2.1 (9)  
 2nd series 0.5 (61) 2.1 (30) 2.2 (12)





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NINA•NIKU Hovedkontor  
Tungasletta 2  
7005 TRONDHEIM  
Telefon: 73 58 05 00  
Telefax: 73 91 54 33

**NINA**  
Norwegian Institute  
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