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THE EFFECT OF ENDURANCE SWIMMING ON GROWTH, BODY COMPOSITION AND CALORIFIC CONTENT OF O-GROUP WHITING (*MERLANGIUS MERLANGUS*, GADIDAE)

by

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Abstract

Juvenile whiting were kept in four groups of 60 specimens each in a flow-through system for two weeks. Two of the four experimental groups were fed with chopped smelt at $7.5\% \text{ bw} \cdot \text{d}^{-1}$, the other two groups were not fed at all. From each fraction (the fed and the non-fed fish) one group was kept swimming at 1 body length/s (BL/s) against a constant current in a raceway; the others remained in group compartments where they swam only marginally. In total there were four groups: two swimming constantly, one of them fed, the other not; and two non-swimming groups, one fed and the other not.

As expected, the condition factor of the groups which were fed increased, whereas that of the non-swimming and non-feeding group decreased. After having swum constantly for two weeks, the feeding fish were slightly heavier than the reference group which was also feeding but not swimming. The better growth of the swimming fish was due to increased muscle growth with a higher dry weight than that of the non-swimming fish. The livers were found to have a lower dry weight, and a lower energy and fat content. Thus, it is concluded that the growth-enhancing effect of prolonged exercise on whiting is not the result of increased water content in the muscles, but reflects true growth of the biomass.

The gross- and net-cost of transport (G-COT, N-COT) for an 18g whiting swimming at 1 Body Length/s (BL/s) (forced swimming) was found to be 5,202 [J/kg/km] (=2434 [J/kg/h]) and 1912 [J/kg/km] (=895 [J/kg/h]) respectively. However, swimming at 0.2-0.3 BL/s (undirected, spontaneous swimming) was more costly than forced swimming and demanded 2561 [J/kg/h] (Gross Cost per Swimming Hour) and 1022 [J/kg/h] (Net-Cost per Swimming Hour). Thus the Net-Cost per Swimming Hour of spontaneous swimming was 14% higher than that of forced swimming.

By means of comparison, no difference between the calculated G-COTs derived from respirometry and the results from direct body calorimetry was found.

Introduction

It has been a widespread belief - mainly in aquaculture - that if the swimming activity of fish is reduced as far as possible, the surplus energy allocated for growth will be maximal. However, throughout the past decade it has become apparent that at least some species of fish seem to grow better when swimming continuously at moderate speeds. This was first demonstrated for salmonid fishes by Greer Walker & Emerson (1978), Nahhas *et al.* (1982), Davie *et al.* (1986) and Leon (1986). Hammer (1993, 1994) demonstrated that maximum growth is achieved when swimming at an average speed of one body length/sec (BL/s). Higher or lower continuous swimming speeds will result in lesser growth. The effect of such endurance swimming on growth may be chiefly sought in hormonal stimulation, as Davison (1989) summarised, and may also have hydrodynamical reasons and behavioural aspects (Webb, 1991; Boisclair & Tang, 1993; Hammer, 1994).

For gadoids Greer Walker (1971), Greer Walker & Pull (1973) and Hammer (1994) demonstrated a similar effect, which, however, appears to be much smaller. As Hammer (1994) showed, the maximum growth of whiting is not found at 1 BL/s as in salmonid species but at a far lower swimming speed: at approximately 0.3 BL/s. Such enhanced growth due to locomotion leads to two questions. Firstly: is the increased growth the effect of a shift of biomass within the body, possibly leading to a reduction of liver reserves with a relatively low water content and also to an increase of muscle tissue with a relatively high water content? Such an internal shift would yield a fake growth, in as much as the growth increase compared to controls would simply reflect a relative increase of water. Secondly: how much energy is really allocated to locomotion while at the same time a weight increase or decrease occurs? A further question that arose was how far the cost of transport (COT) data of whiting from body calorimetry can be put into relation with COT-data received from respirometry.

Materials and Methods

The swimming experiment was conducted at the field station of the Biologische Anstalt Helgoland, on Sylt Is. (FRG, German Bight, North Sea). The fish were caught with the cutter "Seabull" between 10.08 and 11.08. 1993 in the Wadden Sea off List by means of a baby trawl. After being caught, the fish were taken to the experimental room and left undisturbed for 12 hrs. The fish were then disinfected in a tetracycline bath for another 12 hrs. After disinfection the fish were measured and weighed. Only healthy-appearing individuals between 10-15 cm were taken and randomly distributed to the four experimental groups and one control group. The average weights of the individual groups ranged from 17.4 - 19.1g with no significant difference between

the groups (ANOVA, $p=0.1082$). Two of the groups, one swimming at endurance level (*swimming group*), the other left to volitional swimming (*non-swimming group*), were not fed at all. The remaining two groups, again with one swimming and one non-swimming group, were fed with chopped smelt (*Osmerus eperlanus*) with an average calorific content of 22 [J/mg dw] (Hammer, 1994). On average, the ration was 7.5% of the initial body wet weight throughout the two weeks of experiment; the ration was not dynamically adjusted to the growth occurring during the experiment. The chosen ration was supposed to lie just under the *ad libitum* ration which, for this size of fish and kind of food, is 8.1% (Hammer, unpublished data).

group 1 *non-swimming - non fed*

group 2 *non-swimming - fed*

group 3 *swimming - fed*

group 4 *swimming - non fed.*

One experimental basin (diameter 70cm, water depth 40cm) was divided into two identical halves with a plastic screen for group 1 and 2. These two halves contained the *non-swimming* fish. No directed current was installed here, and the volitional movements of the fish were additionally slowed down by hanging obstacles, thus inhibiting the formation of schools or circular migration. Two further basins contained the *swimming groups*. Again, one group was fed, the other not. In these basins, inner cylinders provided an outer raceway (35*40cm), the current being driven by submersible pumps. The fish section of the raceway was separated from the rest by stainless steel screens. Additional screens were installed as turbulence grids. In front of the pumps a brick was hung (Fig. 1); the induced rotation and swinging of the brick divided the turbulent current very evenly. The mean current velocity was 13cm and was measured with a Höntzsch-Anemometer. The chosen current speed of approximately 1BL/s constituted a compromise for the two questions involved: the current speed had to be well under the aerobic maximum, which for whiting of 13cm TL is in the magnitude of 3-3.5 BL/s (Hammer, unpublished data); the current speed also had to be high enough to let the fish expend sufficient amounts of energy in locomotion and simultaneously produce a noticeable difference between the swimming and the non-swimming fish. Also, the swimming speed was supposed to be close enough to the optimal swimming speed for growth to be able to test whether the water and calorific content near U_{gopt} is different than at other swimming speeds. Based on the results given in Fig. 2, and a linear regression through the gadoid data, a growth increase of about 20% at 1BL/s as compared to non-moving controls was expected.

All basins were supplied with fresh sea water (16-17°C), pumped continuously from the Wadden Sea. Before flowing into the experimental basins, the water was aerated and degassed in aeration towers. The light was automatically switched off between 22:00 and 08:00 hrs. In order

to be able to quantify the locomotion of both *swimming* and *non-swimming* groups, the tailbeat frequency (tbf) was repeatedly recorded. The average tbf of the *non-swimming* groups was 0.82 and 0.89, and the tbf of the *swimming* groups was 1.80 and 1.81 respectively. After 14 days the experiment was terminated; the fish were killed in MS222 and instantly deep frozen.

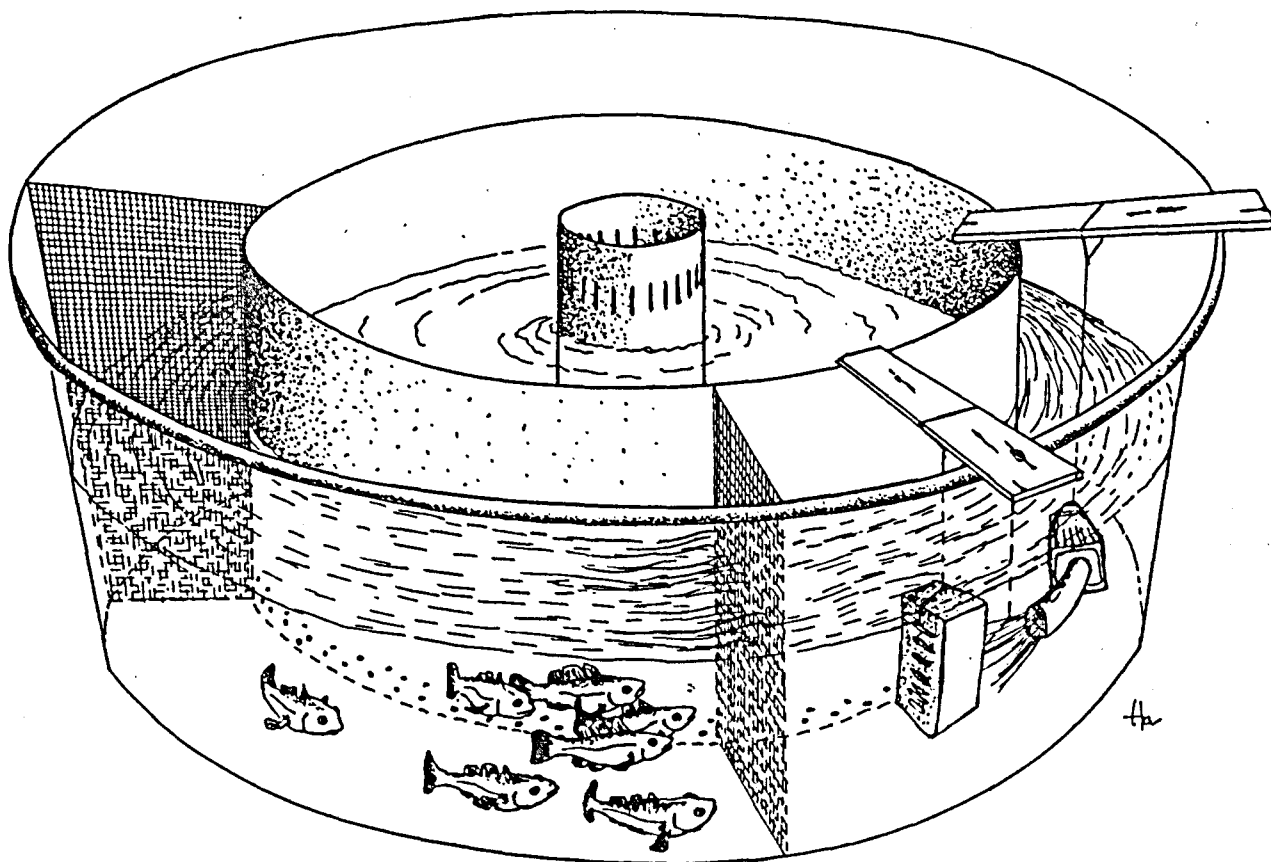


Fig. 1 Experimental setup for the swimming groups

For calorific measurements the fish were thawed, weighed, measured, and then dissected into (1) swimming musculature (the entire fillet, including the red muscles), (2) the liver, and (3) remaining organs including the skull, vertebral column and skin. The samples were dried at 90°C for 48-72h until the weight remained constant. Then the samples were homogenised in an ordinary electric coffee grinder and dried again for 6h at 90°C. Since the livers were not suitable for homogenisation in the coffee grinder, they were mixed with 5 parts benzoic acid before grinding; benzoic acid was also used for calibration of the calorimeter (MK 200, Franz Morat Gerätetechnik) with a constant calorific content of 26430 J/g. Since most of the tissue samples were too small to yield enough dry matter for one measurement, the samples were pooled for measurement. The heat that developed from the reaction of sulphur and nitrogen from the amino acids to sulphuric and nitric acid which develop during measurement, was measured separately (according to DIN

38405, part 5, and DIN 38405, part 9) for calibration. If neglected, this secondary heat development was found to produce an average error of $0.6 \pm 0.11\%$, with no detectable difference between the tissues.

The standard metabolic rate of whiting was calculated with the non-linear function $Q \text{ [mg/h]} = 0.16 * W^{0.88}$ (Purps, 1992). The oxicaloric equivalent of 13.61 was taken from Brett & Groves (1979). The energy equivalents for fat and protein were taken from Elliott & Davison (1975).

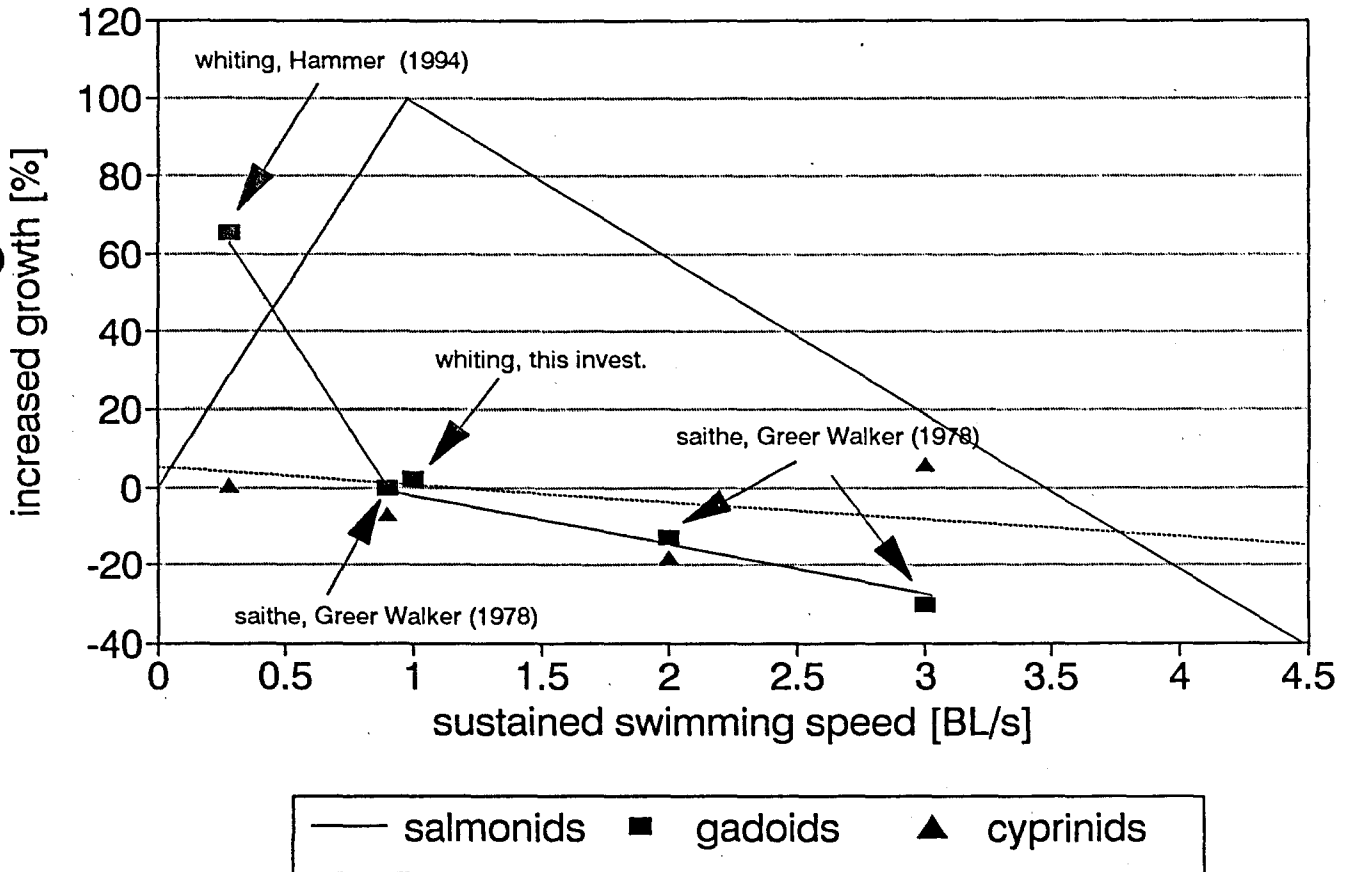


Fig. 2, Change of growth with swimming speed as compared to non-swimming controls.

Results

After 14 days of swimming the feeding group were on average slightly heavier than the non-swimming-feeding group (2.2%ww, 1.6%dw). The water content of the entire fish was equal to that of the non-swimming group (Table 1a). The muscle water content of the swimming group was slightly lower than that of the non-swimming reference group. This also applied to the

average dry matter content and total energy content, whereas the relative energy content was slightly lower than that of the *non-swimming* reference group. Based on these findings, it is possible to reject the hypothesis that the enhanced growth due to swimming could be a proportional shift of liver substance to muscle tissue with a relatively higher water content. However, Table 1c shows that the livers of the *swimming-feeding* group were smaller, with a lower dry weight and a higher water content. The average fat content of the *swimming-feeding* fish (77.1%) had increased as compared to the controls (50.3%), but was lower than the *non-swimming* reference group (78.4%); this appeared to reflect the fuel consumption due to locomotion.

From Tab. 1c it is apparent that throughout the experimental period it was chiefly the liver material of both *non-feeding* groups that was reduced as compared to the control group. In the *non-swimming-non-feeding* group (gr.1), the average dry weight decreased by 64.2%, while the relative energy content decreased only slightly by 2.4%. In absolute terms, the energy content of the liver had decreased by 65%, as compared to the controls. As had been expected, the highest reduction of liver material was found in the *non-feeding-swimming* group. Their dry material decreased by nearly 70%. By contrast, the livers of both *feeding*-groups increased; for the *non-swimming* group by 311% and for the *swimming* group by 269%. The relative and absolute energy content of the livers increased accordingly with a slightly lower increase in the actively *swimming* group. The swimming muscles of the *non-swimming-non-feeding* fish were reduced by 20%, with only slightly changing fat content. For the reference group (*swimming-non-feeding*) a reduction of 23.8% was found. Accordingly, the total energy content of the muscle mass had decreased. However, the specific energy content of the remaining muscle mass was found to be unchanged. The smallest relative changes were found in the "remaining organs" section with a reduction of -13% for group 1 (*non-swimming-non-feeding*) and 22% for group 4 (*swimming-non-feeding*), with only a small reduction in the fat content. The reduction of the absolute energy content of the "remaining organs" section was 17% and 28% respectively demonstrating that, apart from the liver, these parts of the body are an important energy store, out of which not only fat but also to a great extent protein was mobilised.

Both the *non-swimming-feeding* and *non-swimming-non-feeding* fish volitionally moved at 0.85 tb/s. Based on a linear relationship between tbf and swimming speed the *non-swimming* fish had moved at a swimming speed of approximately 0.5 BL/s, which would certainly be an overestimation of the real swimming speed, since tailbeat frequency and swimming speed are not linearly related at the lowest swimming speeds. At these speeds the tailbeats serve not only for directed linear forward motion but also for turns, manoeuvring, breaks, etc. During the experiments an average swimming speed of 0.2-0.3 BL/s was estimated, following direct observations.

From the tissue reductions of the *non-swimming-non-feeding* group an overall reduction of 0.038 [g/ind/d] was calculated. This tissue reduction is due to approximately 83% protein and only 27% fat reduction. Both are equivalent to 2561 [J/kg/h]. The calculated SMR/RMR is 1539 [J/kg/h], which amounts to 60% of the energy reduction. Therefore, a total of 1022 [J/kg/h] remains for this group as net-cost of locomotion at the minimum level at 0.2-0.3 BL/s and all kinds of spontaneous and undirected movements. Thus, the net cost of spontaneous swimming at minimum speed accounts for about 65% of the SMR/RMR.

By comparison, the *non-feeding* but actively *swimming* group at 1BL/s (=forced swimming) had a net cost of transport (N-COT) of only 895 [J/kg/h] (=1.912 [J/kg/km]; 0.457 [Kcal/kg/km]). For an average fish of 18g (ww) with a standard metabolic rate of 113 [mgO₂/kg/h] (=1539 [J/kg/h] ~ 3290 [J/kg/km]) this amounts to a gross cost of transport (G-COT) of 5202 [J/kg/km] (=1.24 [Kcal/kg/km], =2434 [J/kg/h]) and 1912 [J/kg/km] (=895 [J/kg/h]) for the N-COT, respectively (Table 2, Fig. 3). However, the relative cost of swimming at 0.2-0.3 BL/s (undirected, spontaneous swimming) was higher than forced swimming; the demand being 2561 [J/kg/h] (Gross-Cost per Swimming Hour) and 1022 [J/kg/h] (Net-Cost per Swimming Hour). These swimming costs cannot be directly compared with the G-COT and N-COT-values, since the spontaneous movements at minimum swimming speed can not be accurately expressed in units of distance. The Net-Cost per Swimming Hour of the spontaneous swimming was, however, 14% higher than during forced swimming.

Table 1a, energy content of average total fish. Group 1: *non-swimming non-feeding*, 2: *non swimming-feeding*, 3: *swimming-feeding*, 4: *swimming-non-feeding*.

Group	n	av.ww [g]	av.dw [g]	water content [%]	av.energy cont. [J/gdw]	av.energy cont./fish [J]	av. fat cont. [%]
1	60	16.19	2.922	81.95	20123	58799	5.4
2	60	21.47	4.393	79.54	22009	96685	14.0
3	60	21.95	4.461	79.68	21623	96461	12.1
4	60	14.94	2.687	82.02	19869	53387	5.8
control	28	15.95	3.548	77.78	20938	74289	6.6

Table 1b, muscle

Group	n	av.ww [g]	av.dw [g]	water content [%]	av.energy cont. [J/gdw]	av.energy cont./fish [J]	av. fat cont. [%]
1	60	17.369	1.28	82.63	22311	28558	3.6
2	60	10.5	1.979	81.15	22421	44371	5.0
3	60	11.035	2.103	80.94	22349	47000	4.6
4	60	7.016	1.226	82.53	22224	27247	3.7
control	28	7.442	1.6	78.5	22456	35930	4.1

Table 1c, liver

Group	n	av.ww [g]	av.dw [g]	water content [%]	av.energy cont. [J/gdw]	av.energy cont./fish [J]	av. fat cont. [%]
1	60	0.141	0.039	72.34	30058	1172	47.4
2	60	0.783	0.448	42.78	32998	14783	78.4
3	60	0.746	0.404	45.84	30659	12386	77.1
4	60	0.124	0.033	73.39	27151	896	53.0
control	28	0.285	0.109	61.75	30790	3356	50.3

Table 1d, remaining organs

Group	n	av.ww [g]	av.dw [g]	water content [%]	av.energy cont. [J/gdw]	av.energy cont./fish [J]	av. fat cont. [%]
1	60	8.682	1.603	81.54	18134	29069	5.8
2	60	10.184	1.966	80.70	19090	37531	8.3
3	60	10.172	1.954	80.79	18974	37075	6.9
4	60	7.803	1.428	81.70	17678	25244	6.5
control	28	8.241	1.830	77.68	19034	35004	6.3

Discussion

The initial hypothesis was that fibre hypertrophy caused by locomotion leads to a reduction in fat from the liver with a relatively low water content in favour of muscle protein with a relatively low water content. Thus, enhanced growth accompanying endurance swimming could be fake growth if growth is measured in terms of wet weight. The results presented in this paper permit this hypothesis to be rejected. The water content of the entire body is equal in *swimming-feeding* and *non-swimming-feeding* fish. Contrary to the authors' expectations, the *swimming-feeding* fish showed an increased water content in the liver and, *vice versa*, a slightly lower water content in the muscles. However, the assumption that this growth is fake, i.e. merely an increase in the water content, can still be rejected since the livers were smaller than those of the reference group.

The *swimming-feeding* fish were forced to swim continuously at 1 BL/s. The results show that compared to the *non-swimming-feeding* fish they gained 2.2% wet weight. This was less weight gain than expected but coincides with Greer Walker's (1971) results for saithe (*Pollachius virens*) (Fig. 2).

The *non-swimming* groups were both moving volitionally at approximately 0.8 tailbeats/s. The computation of the energy loss of the *non-swimming-non-fed* group showed that the combusted energy was 65% above the computed SMR/RMR derived from respirometry. This indicates that the energy contribution to locomotion on this level is relatively high. Webb (1975) calculated that the power required to swim at any speed is proportional to the speed to the power of 2.8. Using this function the power requirements at 0.2-0.3 BL/s are estimated to be 14% of the energy required for swimming at 1BL/s, which would appear to be a considerable underestimation of the actual cost of transport.

However, the computation of the power requirements of the non-swimming fish still pose a number of problems that are as yet unsolved. The quantification of 0.2-0.3 BL/s is an estimate rather than an accurate measurement. If applying a linear relationship a swimming speed of 0.5 BL/s would be yielded. This would imply that any tailbeat serves the purpose of forward motion, which is certainly not the case. Especially at lowest swimming speeds the fish also exert tail beats spontaneously for turns, accelerations, breaks or positioning, and there is no direct correlation between tbf and tailbeat amplitude. Spontaneous movements are associated with high energy costs. This has been demonstrated for instance by Smit (1965) and Weatherley *et al.* (1982), and was recently quantified by Webb (1991), and Boisclair & Tang (1993) with factors between 3 and 16 as compared to fish swimming in flumes. Yet it still remains questionable whether spontaneous locomotion in the sense used by Webb, Boisclair and Tang can be directly compared with

volitional swimming under the given conditions. With respect to the hanging obstacles in the non-swimming compartments, it seems realistic to assume 0.2-0.3 BL/s as "base speed" for the non-swimming fish. The authors' findings that the hourly energy expenditure of spontaneous swimming is about 114% of the forced and directed swimming expenditure per hour clearly supports the findings of Webb (1991), Boisclair & Tang (1993) and many earlier suggestions.

The energy loss of the *swimming-non-feeding* group was taken here as a direct measure of the Gross-Cost of Transport. How such observations from direct calorimetry can be compared with calculations of the G-COT-values from respirometry is a question that remains to be answered. Tucker (1970) related the G-COT of insects and birds to that of reptiles and mammals. In this comparison fish are represented by one single measurement.

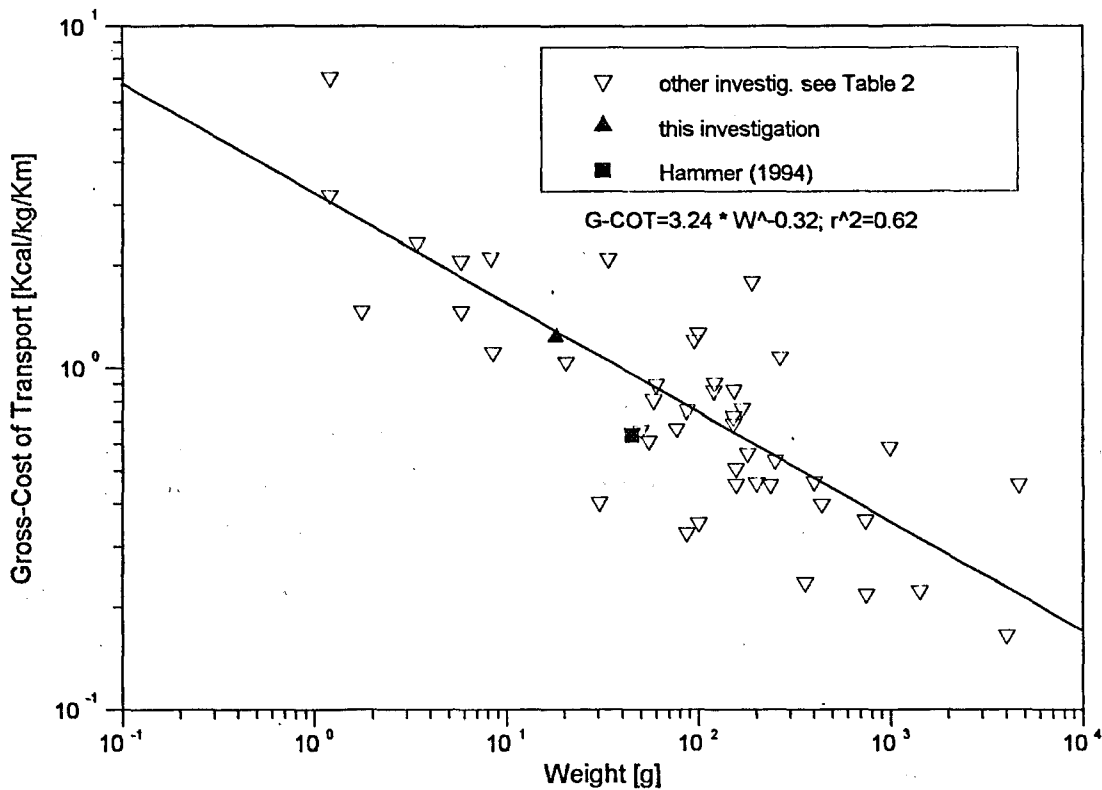


Fig. 3, Gross-Cost of Transport of various fish species against weight. Data from Table 2. Data from Hammer (1994) [■], and this investigation [▲].

Schmidt-Nielsen (1972) and Beamish (1980) followed this line and compared the (apparently gross) COTs of more fish measurements with what appear to be the same measurements for tetrapodes, birds and insects. This comparison has repeatedly been published and discussed in

the context of energy expenditure in the animal kingdom (e.g. Goldspink, 1983; Wieser, 1986). The comparison of the COTs for fish is continued here with the inclusion of more published results and a wider weight range than in previous publications (Fig. 3, Table 2).

Compared to the analogue presentation of Beamish (1980), the scatter of the data has increased. Still, it can be seen clearly that the G-COT of fish decreases exponentially with fish size. This strong exponential relationship is often overlooked since the data are usually presented in a log-log scale. In order to facilitate comparison the same data are given here in a de-log-scale (Fig. 4). For the comparison of the G-COT-values of Schmidt-Nielsen (1972) and Beamish (1980) it must be kept in mind that the costs of transport were (apparently) not normalised to a standard speed. This has led to the G-COTs of different fish at different relative swimming speeds, even though it is known that the swimming efficiency changes significantly with body size and swimming speed (Webb, 1975). For this reason, the authors have in this paper attempted to either select respiration values of swimming speeds near or at 1BL/s (as a standard), or to standardise data to 1 BL/s. Still, this procedure involves problems since swimming at a speed of 1 BL/s is a physiologically different task for a nototheniid than for a fish larva of the tropics. However, for the purpose of this comparison it was decided that a standardisation to 1 BL/s was better than none at all. The same applies to the temperature. For a correct comparison of the respiration values during the swimming experiments, the data ought to be standardised to the physiological optima, which are, unfortunately, in most cases unavailable.

Tucker (1970) and Schmidt-Nielsen (1972) and all other authors using this compilation of data apparently compare the Gross-Costs of Transport. This means that the SMR values are incorporated. However, it is well known that the SMR itself scales strongly with weight, and the question remains accordingly how this scaling effect influences the scaling of the COT with weight.

Nevertheless, the compilation of the G-COT-data serves the purpose of a tentative comparison of the costs of transport. As Table 2 outlines, most of the COT data are gained from respirometry of different kinds. The COT-value from this study, however, is gained from direct calorimetry. As Fig. 3 shows the G-COT-value is obtained from direct calorimetry directly on the regression line of all the values from respirometry studies. This seems to support both approaches in quantifying the COT: respirometry and direct body calorimetry.

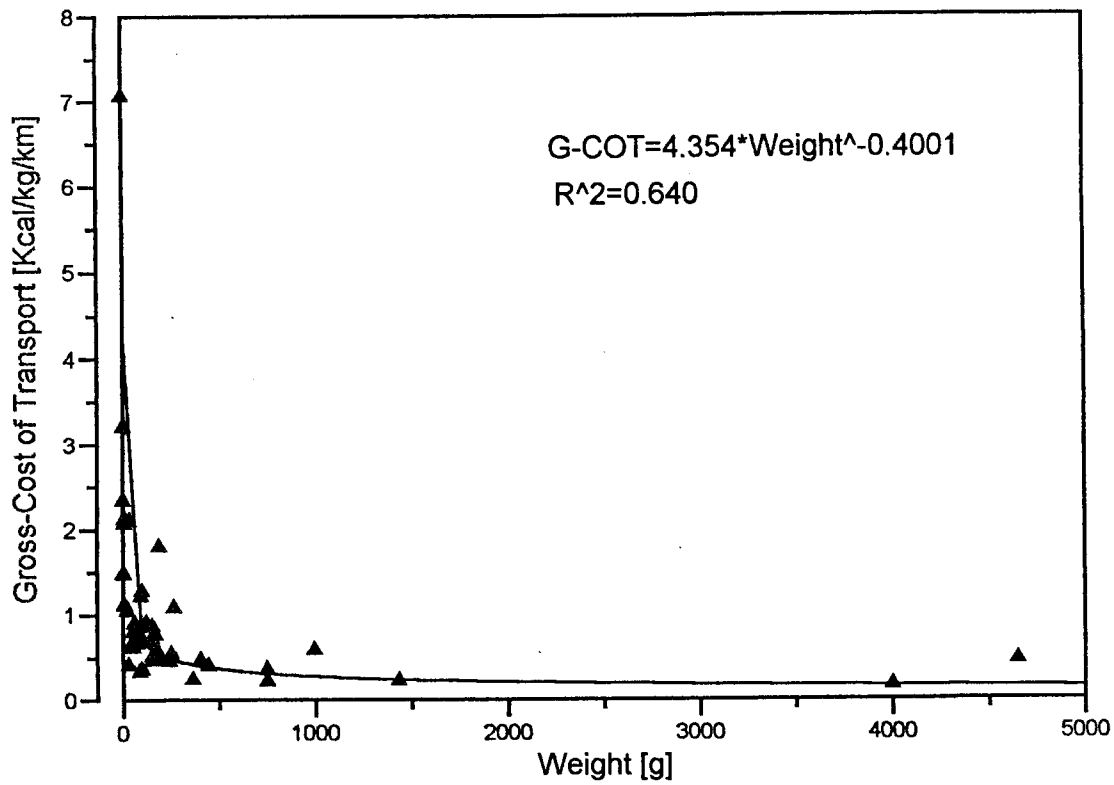


Fig.4, Gross-Cost of Transport of various species of fish (anti-log-scaling). Data from Table 2.

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Author	Species	Weight g	Total l. [cm]	Temp. °C	SMR/RMR [mg O2/kg/h]	SMR/RMR [J/kg/h]	MO2 [J/kg/h]	G-COT [J/kg/km]	G-COT [Kcal/kg/km]	N-COT [J/kg/km]	N-COT [Kcal/kg/km]	Relative Test Speed [BL/s]	Method	Remarks
Averett (1969)	<i>Oncorhynchus kisutch</i>	1,2	5,5	14-15	146	1987	5852	29556	7,06	19522	4,67	1		Data from Puckett & Dill (1984)
Beamish (1970)	<i>Micropterus salmoides</i>	152,5	22,4	30	160	160	2178	3611	0,86	1595	0,38	1,3	tunnel resp	
Beamish (1970)	<i>Micropterus salmoides</i>	180,3	24,1	30	160	160	2178	2357	0,56	1348	0,32	2,5	tunnel resp	
Beamish (1980)	<i>Salvelinus fontinalis</i>	5,8	8,2	15	105	1429	5561	6173	1,48	4587	1,10	3,1	tunnel resp	
Beamish (1980)	<i>Salvelinus alpinus</i>	200	31,6	15	70	953	3137	1936	0,46	1348	0,32	1,42	tunnel resp	
Beamish (1980)	<i>Salvelinus namaycush</i>	5,8	11,5	15	80	1089	13985	8629	2,06	7957	1,90	3,9	tunnel resp	
Brett (1964)	<i>Oncorhynchus nerka</i>	50	18	15	70	953	1794	2768	0,66	1298	0,31	1	Brett resp	
Brett (1965)	<i>Oncorhynchus nerka</i>	3,4	7,7	15	230	3130	4491	9746	2,33	2953	0,71	1,7	Brett resp	
Brett (1965)	<i>Oncorhynchus nerka</i>	8,5	10	15	110	1497	2518	4663	1,11	1891	0,45	1,5	Brett resp	
Brett (1965)	<i>Oncorhynchus nerka</i>	55,2	18,8	15	71	966	1796	2573	0,61	1189	0,28	1,03	Brett resp.	
Brett (1965)	<i>Oncorhynchus nerka</i>	746	41,8	15	71	966	1715	1502	0,36	656	0,16	0,75	Brett resp	
Brett (1965)	<i>Oncorhynchus nerka</i>	1432	53,9	15	44	599	2395	932	0,22	699	0,17	1,33	Brett resp.	
Brett & Sutherland (1965)	<i>Leopomis gibbosus</i>	45	12,7	20	45	613	1241	2718	0,65	1375	0,33	1	Brett resp	
Dutrie (1982)	<i>Limanda limanda</i>	236	29,5	15	18,7	255	2019	1904	0,46	1664	0,40	1	Brett resp	
Dutrie (1982)	<i>Pelichthys flesus</i>	400	31,3	15	39	531	2197	1949	0,47	1477	0,35	1	Brett resp	
Dutrie (1982)	<i>Microstomus kitt</i>	250	28,5	15	51	694	2322	2255	0,54	1581	0,38	1	Brett resp	
Farmer & Beamish (1969)	<i>Tilapia nilotica</i>	77,1	ca.20	25	100	1361	3015	2792	0,67	1541	0,37	ca.1,5	tunnel resp	
Febry & Lutz (1987)	<i>Oreochromis *</i>	58	15,5	28	ca.90	ca.1225	1887	3382	0,81	1186	0,28	1,2	Biazka resp	* Hybrid
Feldmeth & Jenkins (1973)	<i>Salmo gairdneri</i>	100	24,8	11-13,5	57,3	780	3084	5317	1,27	3972	0,95	0,65	Biazka resp	SMR calculated according to Rao (1968)
Furnell (1987)	<i>Anoplopoma fimbria</i>	993	51,8	8,5	58	788	4571	2459	0,59	2028	0,48	1	Brett resp	
Hammer (1994)	<i>Merlangius merlangus</i>	45	19	12	101,3	1379	1826	2670	0,64	654	0,16	0,3	indirect approach	
this investigation	<i>Merlangius merlangus</i>	18	13	16	113	1539		5202	1,24	895	0,21	1	body calorimetry	
Johnston et al. (1991)	<i>Notothenia neglecta</i>	190,1	20,7	1	67,9	924	5606	7523	1,80	6283	1,50	1	Brett resp.	
Kutty (1969)	<i>Liza macrolepis</i>	8,3	10,1	29	150	2042	3226	8839	2,11	3244	0,78	1	fish wheel	
McKries & Power (1992)	<i>Acipenser fluviatilis</i>	4000	80	19	55	744	1966	693	0,17	434	0,10	1	tunnel resp	
Morgan (1972/73)	<i>Salmo trutta</i>	120	20	15	106	1436	2586	3594	0,86	1599	0,38	1	Brett resp	
Morgan (1972/73)	<i>Perca fluviatilis</i>	121	20	15	55	742	2722	3784	0,90	2752	0,66	1	Brett resp	
Muir et al. (1965)	<i>Kuhlia sandvicensis</i>	20,3	12,8	23	87	1182	1609	4365	1,04	1159	0,28	0,8	fish wheel	
Muir et al. (1965)	<i>Kuhlia sandvicensis</i>	60,1	12,8	23	69	937	1200	3745	0,90	821	0,20	0,5	fish wheel	
Neumann et al. (1981)	<i>Morone americana</i>	266	26	15	not stated	-	1399	4518	1,08	-	-	0,33	tunnel resp	
Neumann et al. (1981)	<i>Morone saxatilis</i>	168	21,1	25	not stated	-	5633	3194	0,76	-	-	2,3	tunnel resp	
Neumann et al. (1981)	<i>Morone saxatilis</i>	34	16,4	15	not stated	-	9956	8761	2,09	-	-	1,93	tunnel resp	
Parsons (1990)	<i>Sphyrna tiburo</i>	95	34	25	37,6	512	4142	5070	1,21	2966	0,71	0,82	respirometer	
Parsons (1990)	<i>Sphyrna tiburo</i>	4650	95,4	25	8,1	110	559	1912	0,46	131	0,03	0,5	respirometer	
Pérez-Pinzón & Lutz (1991)	<i>Contropomus undecimalis</i>	1,5-2,0	ass.3	28	79	1075	1102	6174	1,48	152	0,04	1	Biazka resp	recheck with real length data when received
Priede & Holiday (1980)	<i>Pleuronectes platessa</i>	30,6	281	15	51	694	1861	1690	0,40	1060	0,25	1	Brett resp	
Puckett & Dill (1984)	<i>Oncorhynchus kisutch</i>	1,2	5,5	15	146	1987	2164	13417	3,21	1097	0,26	1	respirometer	
Rao (1968)	<i>Salmo gairdneri</i>	100	24,5	15	57	776	2395	1476	0,35	700	0,17	1,84	Biazka resp	
Smit (1965)	<i>Carassius auratus</i>	87	22	20	40	544	2504	3162	0,76	2475	0,59	1	Fish wheel	
Smit (1965)	<i>Carassius auratus</i>	87	22	20	40	544	1096	1383	0,33	696	0,17	1	Biazka resp	
Sooftani & Priede (1985)	<i>Gadus morhua</i>	151,5	26,8	15	132	1802	2923	3028	0,72	1161	0,28	1	Brett tunnel	Length calculated acc to Hawons et al (1985)
Tang (1993)	<i>Salmo selar</i>	ca.750	60	11,2	55	749	1967	911	0,22	564	0,13	1	Wardle doughnut	check real weight with Tang
Tang (1993)	<i>Scomber scombrus</i>	361	35	9,9	48	653	1243	987	0,24	469	0,11	1	Wardle doughnut	weight calcul. acc to Coull et al (1989)
Tyler (1969)	<i>Melanogrammus aeglefinus</i>	156	25	10	58	789	1713	1919	0,46	1035	0,25	1	Biazka resp	
Tyler (1978)	<i>Pollachius virens</i>	152	25,5	15	144	1960	2654	2890	0,69	756	0,18	1	Biazka resp	
Tyler (1978)	<i>Melanogrammus aeglefinus</i>	156	24,8	10	59	803	1905	2134	0,51	1234	0,29	1	Biazka resp	
Tyler (1978)	<i>Gadus morhua</i>	441	36,1	10	86	1170	2178	1675	0,40	774	0,18	1	Biazka resp	
Weatherley et al. (1982)	<i>Salmo gairdneri</i>	471	32,4		90	1225	2042	1750	0,42	700	0,17	1	forced swim chamber	

Table 2, Literature data on the standard metabolic rate (SMR), Gross-Cost of Transport (G-COT) and Net-Cost of Transport (N-COT), relative swimming speed and method.