

EFFECTS OF FEEDING AND STARVATION ON GROWTH AND SWIMMING ACTIVITY IN AN OBLIGATORY AIR-BREATHING FISH

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Abstract

Reared in (tubular) aquaria containing different depths of water, *Ophiocephalus striatus* (0.7 g, 4.5 cm body length), an obligatory air-breathing tropical fish, swam long or short distances to enable themselves to exchange atmospheric air. In each tested depth (2.5, 5.0, 15.5, 31.0 and 40.0 cm) series, one group was starved, while the other was fed *ad libitum* twice a day on fish muscle. In the shallowest water (2.5 cm depth), the feeding group surfaced 1,294 times, travelling 64.7 m at an energy cost of 20.4 mg dry fish substance/g live fish/day, against those exposed to the deepest water (40 cm depth), which expended 35.8 mg/g/day, swimming 1,503.4 m on 1,879 visits to the surface. The starving group surfaced only 482 times, travelling 24.1 m at an expense of 5.8 mg/g/day in the shallowest water, while those at 40 cm depth surfaced 504 times, swimming 403.2 m at an energy cost of 7.4 mg/g/day. Owing to the sustained swimming activity and the consequent fatigue, the test individuals belonging to both groups in all the tested series 'hang' to the surface for a definite interval, repaying the O₂ debt. Observations were also made to assess the duration of 'hanging' to precisely estimate the distance travelled. Irrespective of changes in depths of water, the duration of 'hanging' to surface was only 3.0 hr/day for the feeding groups, while it was as much as 15.5 hr/day for the starving groups. The maximum sustained metabolic level of *O. striatus* reared in 40 cm depth was equivalent to 1.23 ml O₂/g/hr, which is about 2 times higher than the value reported for the active metabolism of swimming *Oncorhynchus nerka* at 15°C in Brett's (1964) respirometer. *O. striatus* reared in 2.5 cm depth fed 32.0 mg and converted 6.7 mg dry food/g live fish/day, while those exposed to the deepest water fed 49.1 mg, but converted only 5.5 mg/g/day. Culturing obligatory air-breathing fishes in shallow waters will be advantageous.

Introduction

There exists an enormous body of literature on metabolism of fishes as studied by oxygen consumption (Fry, 1947, 1957, 1971; Winberg, 1956; Brett, 1970, 1972). Since standard metabolism relates to 'maintenance energy cost' of nonfeeding, nondigesting, nongrowing, nonactive fish, Winberg (1956) rightly appealed for more studies on active metabolism. Studies on active metabolism required exercising apparatus and techniques, such as grids or electrified fields, to ensure a high sustained level of activity (Fry, 1957; Basu, 1959). Of late, more advanced respirometers with exacting hydrodynamic designs were constructed to study the relation between maximum sustained oxygen consumption and swimming speed. These respirometers took the form of recirculating, tubular water tunnels, which could be used in open or closed circuit (Blazka, Volt & Cepela, 1960; Brett, 1964; Farmer & Beamish, 1969).

Feeding-rate and conversion efficiency estimates are considered better parameters for assessing metabolic rates and efficiencies (Kinne, 1960). They provide 1. less restricted maintenance conditions during feeding experiments, 2. the possibility of repeatedly observing one and the same individual over a long period of time, 3. the possibility of measuring the effects of quantitative and qualitative feeding on metabolism (Paloheimo & Dickie, 1966 a,b) and 4. the possibility of measuring total metabolism including the energy expended on part or total anaerobiosis (Kutty, 1968, 1972; Blazka, 1958; however see also Brett, 1973). Food intake is one of the most potent factors, regulating the level of metabolism (Smith, 1935; Beamish & Dickie, 1967; Solomon & Brafield, 1972) and

Table 1. Effects of feeding, starvation and swimming activity on different metabolic parameters in *Ophiocephalus*

	2.5		5.0		Depth of
	Starved	Fed	Starved	Fed	Starved
Number of visits/day	482 ± 24.1	1294 ± 105.6	439 ± 24.4	1317 ± 158.4	446 ± 19.2
Distance travelled (m/day)	24.1 ± 1.20	64.7 ± 5.28	43.9 ± 2.44	131.8 ± 15.84	138.4 ± 5.95
'Hanging' duration (hr/day)	13.2 ± 1.21	7.4 ± 1.09	14.7 ± 1.03	3.2 ± 0.67	15.8 ± 1.18
Corrected distance travelled (m/day)	10.8 ± 1.14	44.7 ± 5.04	17.1 ± 2.34	114.2 ± 15.38	47.5 ± 5.65
Feeding rate (mg/g/day)	-	32.0 ± 4.21	-	35.4 ± 1.47	-
Absorption rate (mg/g/day)	-	27.1 ± 4.21	-	29.8 ± 1.71	-
Conversion rate (mg/g/day)	-5.8 ± 0.21	+6.7 ± 0.52	-5.6 ± 0.29	+7.0 ± 0.27	-6.6 ± 0.20
Metabolic rate* (mg/g/day)	5.8 ± 0.21	20.4 ± 3.69	5.6 ± 0.29	22.8 ± 1.44	6.6 ± 0.20
(ml O ₂ /g/hr) x	0.2 ± 0.01	0.8 ± 0.14	0.2 ± 0.01	0.9 ± 0.06	0.3 ± 0.01
Absorption efficiency (%)	-	85.1 ± 0.53	-	84.0 ± 2.61	-
Conversion efficiency (K ₂) (%)	-	24.0 ± 1.20	-	23.5 ± 1.12	-

* Calculated subtracting the dry weight equivalents of conversion rate from that of absorption

x Calculated considering the expenditure of 4.8 cal energy as equivalent to 1 ml of O₂ uptake

growth (Brown, 1957; Kinne, 1962). Offering different ration levels, Pandian & Raghuraman (1972), and Raghuraman (1973) have recently studied precisely the energy cost of basal, maintenance (basal metabolism + energy cost of alimentation), and active metabolisms in the fish *Tilapia mossambica* as a function of salinity.

For studying active metabolism, as determined by feeding rate and conversion efficiency estimates, we have chosen *Ophiocephalus striatus*, an obligatory air-breathing tropical fish (Johansen, 1970). By rearing the fish in cylindrical aquaria containing different depths of water, the fish were forced to swim longer or shorter distances per unit time for exchanging atmospheric air. For instance, in aquaria containing the maximum (40 cm) water depth offered, the (feeding) fish surfaced once in 46 ± 6.0 sec.; the to and from swimming activity required a total period of 10 ± 1.7 sec. to cover the distance of about 80 cm. Except for the regular interval of about 36 sec. resting at the bottom, the fish was observed to exhibit a maximum sustained swimming activity, i.e. in effect, it was more or less continuously and actively swimming, as if kept in Fry's or Brett's respirometer; in

addition to this, the design of the experiment permitted long term feeding and growth studies.

Material and methods

Fingerlings of *Ophiocephalus striatus* (750 ± 70 mg; 4.5 ± 0.5 cm) were collected from Lake Idumban (Palni), while swimming along their parents; obviously, they belonged to the same brood. They were brought to the laboratory and acclimated to laboratory conditions and feeding schedules. For experiments, cylindrical (7.6 cm diameter) aquaria (capacity: 2.5 l) were chosen to minimize swimming activity in horizontal direction. Five series of individuals were exposed to 2.5, 5.0, 15.5, 31.0 and 40.0 cm water depths (respective water volumes: 0.15, 0.2, 0.7, 1.3 and 1.8 l); in the last 3 series, the test individuals travelled about 6, 13 and 17 times their total body lengths, when they returned to the maximum depth available after each surfacing.

Each series comprised 2 groups: one was starved; the other was offered excess food twice a day, for a period of

striatus. Each value represents the average performance of 3 to 6 individuals maintained for a period of 21 days at 27°C.

water (cm) 15.5	31.0		40.0		
	Fed	Starved	Fed	Starved	Fed
1510 ± 144.0	468 ± 28.8	1798 ± 122.4	504 ± 24.0	1879 ± 146.4	
468.0 ± 44.64	290.2 ± 17.86	1114.5 ± 75.89	403.2 ± 19.20	1503.4 ± 117.12	
3.0 ± 0.84	17.0 ± 0.64	2.5 ± 0.59	14.3 ± 1.20	3.0 ± 1.00	
408.7 ± 43.11	85.1 ± 17.42	999.3 ± 74.00	147.8 ± 18.24	1317.9 ± 112.20	
43.2 ± 4.13	-	47.8 ± 1.36	-	49.1 ± 3.50	
34.8 ± 6.41	-	39.9 ± 1.62	-	41.3 ± 2.90	
+6.2 ± 0.21	-7.1 ± 0.14	+5.6 ± 0.22	-7.4 ± 0.16	+5.5 ± 0.50	
28.6 ± 6.20	7.1 ± 0.14	34.3 ± 1.40	7.4 ± 0.16	35.8 ± 2.40	
1.1 ± 0.24	0.3 ± 0.01	1.3 ± 0.06	0.3 ± 0.01	1.4 ± 0.09	
80.5 ± 3.11	-	83.6 ± 1.60	-	83.9 ± 0.23	
18.0 ± 1.21	-	14.0 ± 1.23	-	13.3 ± 1.30	

rate

(ENGELMANN, 1966); calorific value of *O. striatus* reported to be 4500 cal/g dry weight (PANDIAN, 1967a)

1 hr each; small muscle pieces of the fish *Tilapia mossambica* were used as food. Care was taken to collect unfed food remains with a pipette causing least disturbance to the fish and suitable corrections were made for body fluids lost by the muscle pieces during a 1 hour feeding period. Faeces were collected by filtering the entire aquaria once in 5 days. The 'Sacrifice method' (Maynard & Loosli, 1962) was used for determining the water content of the test individuals of both groups in each series before commencement of the experiments.

Experiments were conducted in a laboratory—where except for feeding and observations—there was no disturbance. The number of visits to the surface by each test individual was observed for a known period of time (10 to 15 min), 4 times a day at 7 am, 1 pm, 7 pm and 11 pm. The distance travelled per individual per day was estimated by multiplying the mean number of visits per unit observation time with twice the depth of water. Observations were made daily for a period of 21 days; since observations were made on 3 to 6 individuals in each of the 2 groups belonging to 5 different series, each value presented in Table 1 represents the average (swimming) performance of a minimum of 336 observations.

Estimations of dissolved oxygen content and pH of each aquarium water was made once in 5 days; oxygen content values ranged between 4.1 and 5.0 ml/l; the pH values between 7.7 and 8.7.

Results and discussion

Table 1 presents data on the effects of different water depths on metabolism and activity of feeding and starving individuals. Individuals of the feeding group increased the number of visits from 1,294 times/day, when kept at a depth of 2.5 cm to 1,879 times/day, when exposed to a depth of 40.0 cm. Correspondingly, the distance travelled increased from about 64.7 m/day to 1,503.4 m/day, i.e. a 23 folded increase. On the other hand, the starving groups surfaced about 467 times/day, irrespective of the changes in the depth of water; however, those exposed to 40.0 cm depth swam 403.2 m/day, against 24.1 m/day by those exposed to 2.5 cm depth.

The increased swimming activity requiring a greater amount of oxygen uptake induced the fish to surface more frequently in the feeding groups; alternatively, the

starving groups maintained a constant number of visits/day; yet, it was not possible for the starved fish in deeper waters to reduce the number of visits, although they had to swim over longer distances. Therefore, the starving fish in 40.0 cm depth increased their swimming activity over a 17 times longer distance, involving an expenditure of 7.4 mg dry fish substance/g live weight/day on the minimum energy cost of living; by comparison those exposed to 2.5 cm depth expended 5.8 mg/g/day.

Close observations made on individuals of *O. striatus* in some preliminary experiments for over 1/2 hr, revealed

that at times the fish were 'hanging' to the surface for a definite period before they returned to the bottom. In addition to the branchial respiration, 'hanging' to the surface permits this obligatory air-breathing fish to exchange gas without vertical movement. Such 'resting duration' may be regarded as a condition, in which the accumulated 'oxygen debt' and the resulting 'fatigue' had reached the maximum threshold (Brett, 1972); the exhausted fish 'hangs' to the surface, repaying its oxygen debt; it exchanges respiratory gases without swimming activities and perhaps active metabolism.

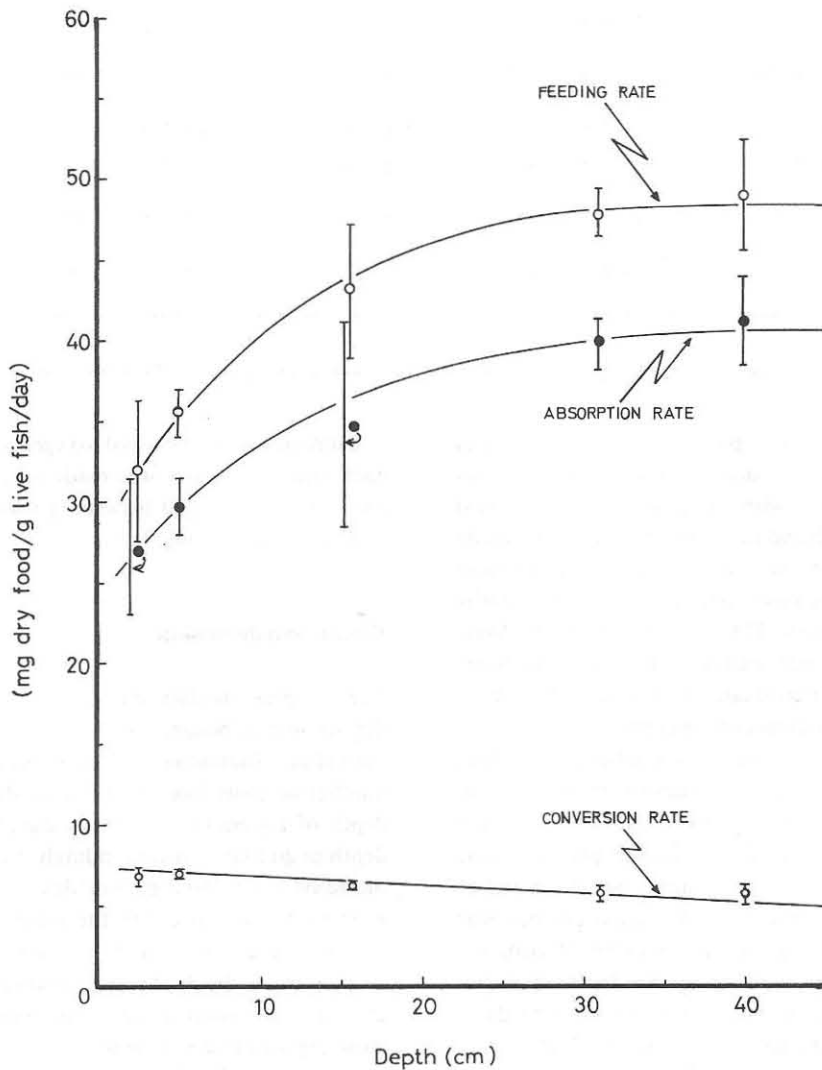


Fig. 1. Effect of water depth on rates of feeding, absorption and conversion in *Ophiocephalus striatus*. Each value represents the average performance of 3 to 6 individuals (mean \pm SD) fed ad libitum, twice a day on muscle pieces of *Tilapia mossambica*.

In order to assess the approximate duration of 'hanging' simultaneous observations were made on the test individuals at least twice a day (at 1 pm and 11 pm) over a period of 20 to 30 minutes. The duration of 'hanging' was only about 3.0 hr/day for feeding fish, while it was as much as about 15.5 hr/day for the starving individuals of the series exposed to 5.0, 15.5, 31.0 and 40.0 cm depths of water; the corresponding values for fish in shallow water (2.5 cm depth) were 7.4 and 13.2 hr/day. Using these values, the data obtained for the distance travelled have been corrected (Table 1).

Since the 'hanging' duration was instant at about 3 hr/day in the feeding groups and at about 15.5 hr/day in the starving groups exposed to 5-40 cm depth, it appears that the differences in the distance travelled have no significant effect on the duration of 'hanging'. However, feeding lets the fish to promptly release energy without frequent built-up of fatigue; in starving fish, the energy expenditure seems to be frequently reduced and fatigue dominates and hanging periods increase in duration. The duration of 'resting period' increases with increasing intensity of starvation; for instance, the starving fish exposed to 40 cm depth 'hanged' to the surface for an average period of 8.2 hr/day during the first 5 days of starvation. From the 10th day of fasting, the fish prolonged the 'resting period' by 'hanging' to the surface for 17.4 hr/day (Vivekanandan, unpublished).

Feeding rate steadily increased from 31.0 ± 4.21 mg dry food/g live fish/day in fish exposed to 2.5 cm depth to 49.1 ± 3.50 mg dry food/g live fish/day in fish exposed to 40.0 cm depth. Feeding rates of fish exposed to 31.0 and 40.0 cm fish are statistically not different ($t = 0.50$; $P > 0.10$); the same is true in regard to the number of visits ($t = 0.73$; $P > 0.10$). The initial steep increase in food consumption approached an asymptote, when the fish was exposed to over 30.0 cm water depths (Fig. 1). Food absorption efficiency averaged 83.4% and did not appreciably vary between these groups (despite more than 50% increase in ration levels; see also Gerking, 1955, 1971; Pandian, 1967 b); hence the trend obtained for absorption rate as a function of depth of water is parallel to the one obtained for feeding rate against depth of water.

Both conversion rate and conversion efficiency (K_2) decreased from 6.7 mg dry food/g live fish/day and 24.0% in those exposed to 2.5 cm depth to 5.5 mg dry food/g live fish/day and 13.3% in those exposed to the maximum tested depth of water, respectively. Consequently, cultivation of obligatory air-breathing fishes like *O. striatus* in deep waters would result in poor conversion efficiencies

and slow growth rate, despite the increased food consumption. Fish exposed to shallow water (2.5 cm depth) need to swim only 64.7 m/day at an expense of 20.4 mg/g/day, those in the deepest water must swim 1,503.4 m/day and spend 35.8 mg/g/day. Again, the difference in the amount of energy spent on metabolic processes by test groups exposed to 31 and 40 cm is not statistically significant ($t = 0.54$; $P > 0.10$) and hence, an expenditure of 35.8 mg/g/day, which is equivalent of 1.4 ml O_2 /g/hr on metabolic processes, may be considered as 'the maximum sustained active metabolic level' (Brett, 1972) of the fish *O. striatus* under the present experimental conditions. This value may be compared with that of 0.63 ml O_2 /g/hr reported by Brett (1964) for active metabolism of 50 g sockeye salmon *Oncorhynchus nerka* at 15°C; Brett's value for active metabolism of *O. nerka*, as estimated by oxygen uptake, is one of the highest values reported in the literature, but is less than half of that assessed for *Ophiocephalus striatus* from feeding rate-conversion estimates. The possible reasons for this discrepancy are discussed in the ensuing paragraphs.

Both fed and starved groups of all test series were starved one day before the beginning of the experiments. While the starving groups progressively reduced their minimum

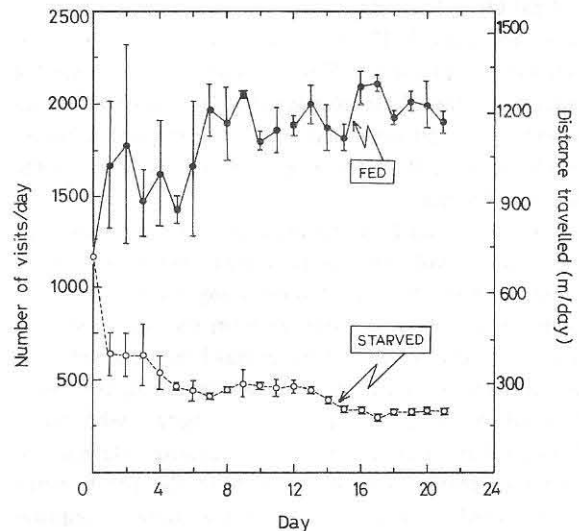


Fig. 2. Effects of feeding and starvation on the number of visits to the surface for exchange of atmospheric air and the distance travelled by the fish *Ophiocephalus striatus* reared in aquaria containing 31.0 cm depth of water at 27°C. Each value represents the average performance of 3 to 6 individuals (mean \pm SD), observed for 10 to 15 minutes, 4 times a day, for a period of 21 days.

activities, the feeding groups steadily increased their locomotory performance (e.g. from the series in 31 cm depth; Fig. 2). Consequently, feeding rates modify swimming activity directly; but changes in water depth only secondarily modifies the effects of feeding levels on swimming activity. Scientists like Brett (1964), who used more advanced respirometers for measuring maximum sustained oxygen consumption of swimming fish have considered active metabolism as the level of O_2 uptake displayed by the test individuals starved for more than 36 hours. On the very 2nd day of the experiment, the distance travelled by the feeding group of the series exposed to 31 cm depth was over 1,101 m/day, as against 408 m/day by the starving group (Fig. 2), i.e. the swimming activity of the feeding group was over $2\frac{1}{2}$ times higher than those just starved for 2 days. If the difference between the activity levels of the feeding and starving *O. striatus* was true for *Oncorhynchus nerka* too, the maximum sustained O_2 uptake level (0.63 ml O_2 /g/hr; Brett, 1964) of the starved (for 2 days) swimming *O. nerka* is likely to be an underestimate by a factor of about 2.5. In fact, Muir, Nelson & Bridges (1965) have shown that oxygen consumption of the aholehole, *Kuhlia sandvicensis* (44 g), maintained at a constant level of activity (swimming at a speed of 0.23 body lengths/sec) decreased from about 0.14 ml O_2 /g/hr just after feeding to about 0.07 ml O_2 /g/hr, 2 days after feeding. Feeding (Smith, 1935; Solomon & Brafield, 1972) and the consequent alimentation processes (Raghuraman, 1973) elevate the metabolism; had Brett estimated the O_2 uptake of feeding *O. nerka*, it is possible that the fish displayed a higher metabolic level than the one reported by him for the starving *O. nerka*.

For want of data on the quantities of ammonia, urea and other soluble excreta produced, metabolic rate of *O. striatus* was determined subtracting faecal losses and change in dry body substances from the dry food consumed, i.e. absorbed food energy has been assumed to be equivalent to metabolizable food energy. From the values reported by Solomon & Brafield (1972), who made simultaneous measurements on feeding, defecation, excretion, respiration and growth of the perch *Perca fluviatilis* fed a ration in excess of maintenance requirements of *Gammarus pulex* at 14°C, the mean excretory energy lost per unit weight of consumed food was recalculated to amount 9.85% (of the 3 suitable values reported by them, one unusually high value 31.4% was not considered). Therefore, the metabolic rate of a feeding group of *O. striatus* exposed to different depths may be an over-

estimate by about 10%; for instance, the metabolised food energy for the feeding group exposed to 40 cm depth, which absorbed food at the rate of 41.3 mg/g/day, will be 37.1 mg/g/day and the consequent corrected metabolic rate should be 1.23 ml O_2 /g/hr. By comparison, this high metabolic rate of *O. striatus* is about 2 times higher than Brett's value (0.63 ml O_2 /g/hr) for *O. nerka*. It may also be pointed out that the *O. striatus* used in the present study weighed only 0.75 g and *O. nerka* used by Brett 50 g. It is well known that with increasing body weight metabolic rate decrease (see Zeuthen; 1947; Pandian, 1967 a).

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