SURFACING ACTIVITY AND FOOD UTILIZATION IN A TROPICAL AIR-BREATHING FISH EXPOSED TO DIFFERENT TEMPERATURES*

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Abstract

Reared in tubular aquaria containing different depths of water (2.5, 5.0, 15.5, 31.0 and 40.0 cm), the obligatory air-breathing fish *Ophiocephalus striatus* (760 mg; 4.5 cm L) was forced to swim vertically a longer or shorter distance per surfacing. Interaction of temperature (17, 22, 27, 32 and 37°C) and aquarium depth reveals that surfacing frequency of the fish, fed *ad libitum* on *Tilapia* muscle, increased with increasing aquarium depth, but the increase was significant only at 27 and 32°C; in the starving series, the frequency was not depth-dependent at any temperature. Owing to the sustained surfacing activity and the consequent fatigue, the test individuals 'hung' to the surface for a definite period. Hanging frequency was temperature-dependent, but not a depth-dependent activity either in the starving or feeding series. At any temperature and aquarium depth, the feeding series hung more frequently than the starving series. Hanging duration increased from about 1 hr/day in either series at 17°C to 6 and 18 hr/day in the feeding and starving series at 37°C. At any tested temperature, distance swum by the feeding and starving series was a depth-dependent activity. The feeding series at 32°C exhibited the maximum swimming speed of 2 L/sec for 4.8 hr/day in the 40 cm depth. With increasing temperature and depth, feeding rate increased (from 24 to 225 g cal/g live fish/day); between 17 and 27°C, it was a temperature-dependent activity. The highest rate (47 g cal/g/day) and efficiency (27%) of conversion were observed at 32°C; whereas the efficiency was depth-dependent, the rate was not. Oxygen uptake was a temperature-dependent activity; aquarium depth played a secondary role. Briefly, *O. striatus* in deeper aquaria consumed significantly more food and converted lesser, as it surfaced more frequently and swam longer distance, dissipating more energy on metabolism and swimming activity. Hence, culturing *O. striatus* in shallow waters at the optimum temperature of 32°C will be advantageous.

Introduction

In tropical countries like India, where availability of freshwater is limited, air-breathing fishes may be chosen for aquaculture, as they thrive in shallow waters deficient in oxygen. However, the advantageous air-breathing habit of these fishes and the consequent need to surface more or less at regular intervals may impose a considerable drain of energy, which otherwise could have been channelled into fish production. Aspects of optimizing energy drain due to surfacing activity have recently received considerable attention for a number of Indian air-breathing fishes (Arunachalam *et al.,* 1977; Pandian & Vivekanandan, 1976; Pandian *et al.,* 1977; Vivekanandan *et al.,* 1976, 1977). These authors have recommended culturing air-breathing fishes in shallow waters.

However, the shallow waters in the tropics undergo considerable diurnal and seasonal changes in temperature (Jhingran, 1975). Publication concerning the temperature effects on surfacing activity and food utilization is totally wanting; as such, almost no information is available on temperature effects on food utilization of tropical fishes. This paper represents one of the series of an extensive

of behavioural resting period, during which *O. striatus* exchanges atmospheric air without undertaking vertical movement, is termed 'hanging'.

Distance travelled

Actual distance swum by the fish per unit time of observation or day (excluding 'hanging' duration) to exchange atmospheric air, i.e. the distance swum, while ascending from the bottom of the aquarium to the water surface, and descending to the maximum depth available after each surfacing. At times, the fish ascends 3/4 of the maximum distance, but returns to the bottom without exchanging atmospheric air. This type of sporadic, random swimming activity is not taken into account in the present study.

a) Swimming activity: Overall vertical distance swum (m/day) by the fish for exchanging atmospheric air per unit time of observation or day.

b) Swimming speed: Distance swum by the fish for surfacing per unit time (sec), which is expressed in body length (L)/sec, following Bainbridge (1958).

Observations and calculations

At any one time, 6 individuals were observed using a separate stop watch and digital counter for each test fish. Observations on the number of surfacing by each test individual were carried out every day for a known period of usually 15 min (or for a longer period, during which a minimum of 5 surfacings were observed), 4 times a day at 7 am, 1 pm, 7 pm and 11 pm. These values were added and the number of surfacing/day was calculated.

A recording device like the one suggested by Saksena (1975) could not be used because, during the hanging, the dorsal fin of *O. striatus,* which extends about 3/4 of its body length, projects above the water surface. This leads to false recording, when the fish is not actually surfacing.

Observations on the hanging frequency and hanging duration were made for 15 min (or for a minimum of 3 hanging frequencies), subsequent to observation on surfacing; these values were multiplied for a unit time (day).

The distance travelled (m/day) per individual per day was estimated by multiplying the mean number of surfacing/day with twice the depth of water. Further, it was corrected by deducting the hanging duration (hr/day).

II. Definition of terms related to food utilization

The scheme of energy balance followed in the present work is that of the IBP formula (Petrusewicz & MacFadyen, 1970) usually represented as $C = P + R + F + U$, where C is the food energy consumed, P the growth, R the energy lost as heat due to metabolism, F the faeces and U the nitrogenous excretory products. Quantitative estimations of the C were made in terms of g calorie. The quantity of absorbed food energy (Ae) was estimated by subtracting the F from the C, and that of the P by subtracting the initial energy content of the individual at the commencement of the experiment from the final energy content of the individual at the end of the experiment. The term conversion has been used to refer to growth, i.e. the P of the IBP terminology.

As the U was not estimated in the present study, the value for the perch *Perca fluviatilis* (Solomon & Brafield, 1972) was used for all the experiments; 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).

As the C, P, F and U are known, metabolism (R = respiration) can be calculated relating it to per unit initial live weight (g) of the fish per unit time (day). To express metabolism as ml O_2 uptake, 4.8 g cal energy was considered as equivalent to 1 ml of O_2 uptake (Engelmann, 1966).

The closed (● ■ • ▼ ▲ = fed series) and open (▫ □ ○ ▽ ◌ = starved series) symbols in all the figures represent the aquarium depths of 2.5, 5.0, 15.5, 31.0 and 40.0 cm, respectively.

Results

Surfacing activity

At any tested temperature, feeding series surfaced to exchange atmospheric air more frequently with increasing aquarium depth (Fig. 1); however, the increase in surfacing frequency was not statistically significant at 17, 22 and 37°C (Tables II, III, and VI); the 't' values obtained for the surfacing frequency of the 2.5 cm vs 40 cm depth groups were 2.153 ($P > 0.05$) at 17°C, 2.347 ($P > 0.05$) at 22°C and 1.332 ($P > 0.05$) at 37°C. The 't' values calculated for the corresponding depth groups at 27 and 32°C were 6.482 ($P < 0.001$) and 4.470 ($P < 0.01$), respectively and were highly significant. Therefore, the surfacing is a depth-dependent activity only within the narrow range of temperature between 27 and 32°C.
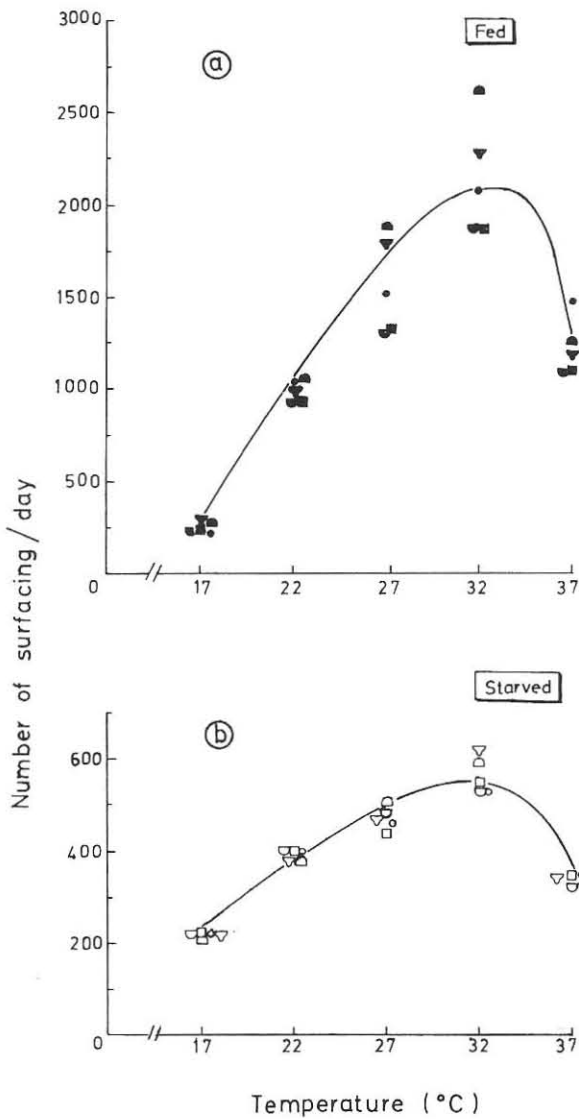
Fig. 1. Effects of temperature and depth of water on number of surfacing of the fed and starved *Ophiocephalus striatus*.

different depths surfaced 240 time/day and the minor differences observed between the corresponding groups among the two series were not statiscally significant (e.g. at 40 cm depth: t = 2.261; P > 0.05). At all other tested temperatures, the frequency of the feeding series was 2 to 5 times more than that of the starving series; for instance, the frequency averaged to 389, 504, 594 and 326 time/day for the starving series at 22, 27, 32 and 37°C, respectively, and the corresponding values for the groups exposed to 40 cm depth of the feeding series were 1054, 1879, 2616 and 1203 time/day, respectively.
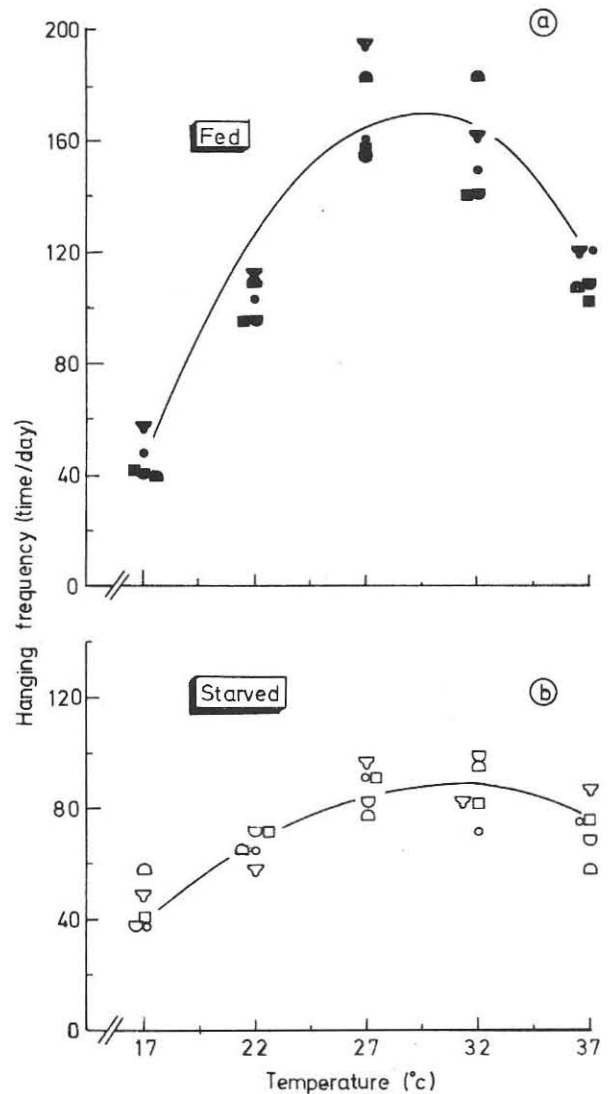
Fig. 2. Effects of temperature and depth of water on hanging frequency of the fed and starved *Ophiocephalus striatus*.

Similar analysis of the data obtained for the starving series exposed to different depths of water revealed that surfacing frequency was not a depth-dependent activity in the starving series at all tested temperatures (Fig. 1); however, the fish progressively increased the frequency from 222 time/day (mean of means obtained for the starving depth groups) at 17°C to 563 time/day at 32°C. At 37°C, the frequency significantly decreased to a level (336 time/day) lower than that at 22°C (Fig. 1).

At 17°C, the starving and feeding series exposed to

148

Table II. Effects of feeding, starvation and aquarium depth on different metabolic parameters in *Ophiocephalus striatus* (815 ± 90 mg). Each value represents the average performance of 3 to 6 individuals (mean ±SD) maintained for a period of 35 days at 17°C

Depth of water (cm)

Parameters	2.5		5.0		15.5		31.0		40.0	
	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved
Number of surfacing/day	235 ± 21.5	223 ± 23.0	235 ± 32.0	222 ± 20.1	245 ± 29.9	221 ± 31.0	284 ± 21.5	226 ± 40.0	283 ± 39.0	219 ± 41.0
Hanging frequency (time/day)	41 ± 2.8	39 ± 3.6	42 ± 4.4	41 ± 7.3	48 ± 4.9	39 ± 2.6	58 ± 3.4	49 ± 9.7	40 ± 9.3	58 ± 6.1
Hanging duration (hr/day)	0.5 ± 0.04	1.0 ± 0.10	0.5 ± 0.10	1.0 ± 0.11	0.7 ± 0.01	1.1 ± 0.02	0.8 ± 0.10	1.1 ± 0.10	0.9 ± 0.10	1.1 ± 0.10
Distance travelled (m/day)	12 ± 1.1	11 ± 1.0	23 ± 3.2	21 ± 2.0	74 ± 9.0	65 ± 9.6	170 ± 12.9	134 ± 23.6	218 ± 30.1	168 ± 31.5
Feeding rate (g cal/g/day)	23.6 ± 1.99	---	23.6 ± 1.57	---	30.4 ± 3.80	---	42.8 ± 2.00	---	45.2 ± 0.51	---
Absorption rate (g cal/g/day)	22.9 ± 1.94	---	23.0 ± 1.70	---	29.6 ± 3.80	---	41.9 ± 2.09	---	14.1 ± 0.70	---
Conversion rate (g cal/g/day)	+3.1 ± 0.15	−0.6 ± 0.10	+3.6 ± 0.10	−1.0 ± 0.17	+2.9 ± 0.25	−1.8 ± 0.17	+0.7 ± 0.61	−1.5 ± 0.10	+0.5 ± 0.41	−2.1 ± 0.17
Metabolic rate (g cal/g/day)	17.8 ± 1.80	0.6 ± 0.10	17.5 ± 1.74	1.0 ± 0.17	24.0 ± 3.60	1.8 ± 0.17	37.1 ± 2.60	1.5 ± 0.10	39.2 ± 1.07	2.1 ± 0.17
Metabolic rate (ml O_2/g/hr)	0.15 ± 0.021	0.01 ± 0.00	0.15 ± 0.019	0.01 ± 0.002	0.21 ± 0.031	0.01 ± 0.002	0.33 ± 0.019	0.01 ± 0.001	0.35 ± 0.013	0.01 ± 0.001
Absorption efficiency (%)	96.9 ± 0.60	---	97.5 ± 0.76	---	97.3 ± 0.51	---	97.8 ± 0.55	---	97.7 ± 0.85	---
Conversion efficiency (K_2)(%)	13.5 ± 0.50	---	15.8 ± 1.57	---	10.0 ± 0.41	---	1.7 ± 1.01	---	1.1 ± 0.95	---

Table III. Effects of feeding, starvation and aquarium depth on different metabolic parameters in *Ophiocephalus striatus* (790 ± 61 mg). Each value represents the average performance of 3 to 6 individuals (mean ± SD) maintained for a period of 28 days at 22°C

Depth of water (cm)

Parameters	2.5		5.0		15.5		31.0		40.0	
	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved
Number of surfacing/day	923 ± 25.2	400 ± 40.1	929 ± 40.0	398 ± 13.2	1041 ± 149.0	404 ± 16.5	951 ± 73.8	384 ± 35.4	1054 ± 104.0	389 ± 25.0
Hanging frequency (time/day)	96 ± 10.8	72 ± 16.2	96 ± 18.1	72 ± 10.1	104 ± 17.6	65 ± 18.1	113 ± 13.9	59 ± 10.4	110 ± 18.9	64 ± 9.7
Hanging duration (hr/day)	6.9 ± 0.10	10.5 ± 0.60	6.7 ± 0.10	10.2 ± 0.85	7.9 ± 0.78	10.4 ± 0.20	7.3 ± 0.50	11.7 ± 0.50	9.0 ± 0.51	11.1 ± 0.10
Distance travelled (m/day)	33 ± 0.9	11 ± 1.5	67 ± 3.1	23 ± 0.7	199 ± 27.1	71 ± 2.6	411 ± 3.2	122 ± 11.5	527 ± 52.0	167 ± 10.7
Feeding rate (g cal/g/day)	79.8 ± 5.60	---	87.3 ± 8.81	---	100.3 ± 9.34	---	103.7 ± 12.5	---	110.7 ± 11.75	−±−
Absorption rate (g cal/g/day)	77.8 ± 5.44	---	84.9 ± 7.99	---	97.3 ± 8.67	---	100.8 ± 11.63	---	106.8 ± 10.31	---
Conversion rate (g cal/g/day)	+17.4 ± 2.54	−8.9 ± 1.25	+13.9 ± 4.33	−10.0 ± 0.35	+16.3 ± 2.43	−9.9 ± 0.98	+11.9 ± 2.49	−11.8 ± 2.11	+13.1 ± 0.70	−12.1 ± 1.25
Metabolic rate (g cal/g/day)	54.3 ± 4.00	8.9 ± 1.25	64.0 ± 6.31	10.0 ± 0.35	72.9 ± 7.22	9.9 ± 0.98	80.1 ± 11.23	11.8 ± 2.11	84.4 ± 9.61	12.1 ± 1.25
Metabolic rate (ml O_2/g/hr)	0.49 ± 0.03	0.07 ± 0.00	0.56 ± 0.11	0.09 ± 0.00	0.63 ± 0.06	0.09 ± 0.01	0.70 ± 0.10	0.10 ± 0.02	0.73 ± 0.08	0.11 ± 0.01
Absorption efficiency (%)	97.4 ± 0.45	---	97.5 ± 0.51	---	97.0 ± 0.50	---	97.3 ± 0.69	---	96.4 ± 0.79	---
Conversion efficiency (K_2) (%)	22.4 ± 2.29	---	16.4 ± 5.73	---	16.8 ± 1.92	---	11.8 ± 2.60	---	12.3 ± 0.55	---

Table IV. Effects of feeding starvation and aquarium depth on different metabolic parameters in *Ophiocephalus striatus*(750 ± 70 mg). Each value represents the average performance of 3 to 6 individuals (mean ± SD) maintained for a period of 21 days at 27°C

	Depth of water (cm)									
	2.5		5.0		15.5		31.0		40.0	
Parameters	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved
Number of surfacing/day	1294 ± 105.6	482 ± 24.1	1317 ± 158.4	439 ± 24.4	1510 ± 144.0	446 ± 19.2	1798 ± 122.4	468 ±:28.8	1879 ± 146.4	504 ± 24.0
Hanging frequency (time/day)	155 ± 16.9	83 ± 21.2	158 ± 18.2	92 ± 13.8	160 ± 17.7	91 ± 9.9	195 ± 23.4	97 ± 12.8	183 ± 10.0	78 ± 11.5
Hanging duration (hr/day)	7.4 ± 1.09	13.2 ± 1.21	3.2 ± 0.67	14.7 ± 0.94	3.0 ± 0.84	15.8 ± 1.18	2.5 ± 0.59	17.0 ± 0.64	3.0 ± 1.00	14.3 ± 1.20
Distance travelled (m/day)	45 ± 4.0	11 ± 0.5	114 ± 6.9	17 ± 0.9	409 ± 38.7	47 ± 2.0	999 ± 74.7	85 ± 5.2	1315 ± 102.7	163 ± 7.0
Feeding rate (g cal/g/day)	144.2 ± 19.07	---	160.5 ± 6.66	---	196.0 ± 18.7	---	216.2 ± 6.16	---	222.6 ± 15.86	---
Absorption rate (g cal/g/day)	137.9 ± 21.09	---	151.3 ± 5.34	----	190.0 ± 19.21	---	205.5 ± 6.46	---	210.1 ± 17.7	---
Conversion rate (g cal/g/day)	+28.2 ± 3.30	−22.5 ± 0.81	+33. ± 5.53	−20.5 ± .106	+24.7 ± 3.91	−25.3 ± 0.77	+26.5 ± 1.47	−27.3 ± 0.54	+26.5 ± 2.23	−28.3 ± 0.61
Metabolic rate (g cal/g/day)	98.8 ± 18.75	22.5 ± 0.81	106.2 ± 5.47	20.5 ± 1.06	148.8 ± 9.61	25.3 ± 0.77	161.1 ± 7.90	27.3 ± 0.54	165.3 ± 14.56	28.3 ± 0.61
Metabolic rate (ml O_2/g/hr)	0.86 ± 0.18	0.20 ± 0.01	0.92 ± 0.05	0.18 ± 0.01	1.29 ± 0.81	0.22 ± 0.01	1.41 ± 0.07	0.24 ± 0.01	1.44 ± 0.13	0.25 ± 0.01
Absorption efficiency (%)	95.6 ± 0.18	---	94.3 ± 0.79	---	96.9 ± 0.91	---	95.0 ± 0.50	---	94.5 ± 0.10	---
Conversion efficiency (K_2) (%)	20.4 ± 1.08	---	22.1 ± 3.30	---	13.0 ± 0.10	---	13.0 ± 1.00	---	12.6 ± 1.27	---

Table V. Effects of feeding, starvation and aquarium depth on different metabolic parameters in *Ophiocephalus striatus* (700 ± 37 mg). Each value represents the average performance of 3 to 6 individuals (mean ± SD) maintained for a period of 21 days at 32°C

	Depth of water (cm)									
	2.5		5.0		15.5		31.0		40.0	
Parameters	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved
Number of surfacing/day	1860 ± 190.0	530 ± 51.5	1857 ± 205.5	547 ± 70.7	2074 ± 173.9	527 ± 55.3	2272 ± 244.4	615 ± 86.8	2616 ± 278.7	594 ±73.2
Hanging frequency (time/day)	142 ± 2.8	99 ± 6.9	141 ± 9.3	82 ± 10.2	150 ± 13.5	72 ± 14.5	126 ± 12.9	83 ± 10.8	184 ± 7.5	96 ± 9.7
Hanging duration (hr/day)	3.2 ± 0.61	15.0 ±1.42	3.2 ± 0.34	14.4 ± 1.52	3.0 ± 0.91	15.0 ± 1.72	3.4 ± 0.97	16.8 ± 1.45	4.3 ± 0.76	16.8 ± 0.92
Distance travelled (m/day)	81 ± 9.3	10 ± 1.0	161 ± 20.3	30 ± 2.8	563 ± 49.7	61 ± 2.1	1220 ± 127.6	114 ± 26.0	1721 ± 161.6	143 ± 22.0
Feeding rate (g cal/g/day)	180.4 ± 28.57	---	189.7 ± 13.91	−±−	212.4 ± 30.33	---	225.3 ± 31.17	---	224.8 ± 8.67	---
Absorption rate (g cal/g/day)	172.7 ± 26.68	---	181.1 ± 29.27	---	206.4 ± 30.18	---	215.9 ± 25.40	---	216.2 ± 9.05	---
Conversion rate (g cal/g/day)	+46.6 ± 5.03	−22.1 ± 0.69	+38.1 ± 3.62	−23.5 ± 3.47	+31.8 ± 2.59	−25.5 ± 2.00	+31.2 ± 1.44	−25.3 ± 0.91	+34.5 ± 5.46	−29.3 ± 1.25
Metabolic rate (g cal/g/day)	113.5 ± 18.98	22.1 ± 0.69	128.7 ± 24.03	23.5 ± 3.47	157.2 ± 26.30	25.5 ± 2.00	166.3 ± 21.69	25.3 ± 0.91	163.6 ± 8.59	29.3 ± 1.25
Metabolic rate (ml O_2/g/hr)	1.00 ± 0.17	0.20 ± 0.01	1.12 ± 0.21	0.20 ± 0.01	1.37 ± 0.23	0.22 ± 0.02	1.44 ± 0.19	0.22 ± 0.01	1.43 ± 0.08	0.25 ± 0.01
Absorption efficiency (%)	95.5 ± 0.56	---	95.5 ± 0.10	---	97.2 ± 0.98	---	95.9 ± 2.32	---	96.1 ± 0.78	---
Conversion efficiency (K_2) (%)	27.4 ± 1.52	---	21.3 ±2.06	---	15.6 ± 2.00	---	14.5 ± 1.69	---	15.9 ± 1.91	---

Table VI. Effects of feeding, starvation and aquarium depth on different metabolic parameters in *Ophiocephalus striatus* (735 ± 65 mg). Each value represents the average performance of 3 to 6 individuals (mean ± SD) maintained for a period of 21 days at 37°C

Parameters	Depth of water (cm)									
	2.5		5.0		15.5		31.0		40.0	
	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved
Number of surfacing/day	1091 ± 119.0	322 ± 61.0	1096 ± 106.0	347 ± 65.0	1470 ± 141.5	347 ± 51.6	1189 ± 285.1	336 ± 63.9	1203 ± 119.1	326 ± 40.4
Hanging frequency (time/day)	109 ± 9.9	69 ±8.5	103 ± 6.8	76 ± 8.3	121 ± 8.2	75 ± 10.8	121 ± 8.0	87 ± 6.3	108 ± 1.2	68 ± 8.7
Hanging duration (hr/day)	5.3 ± 0.10	17.5 ± 0.32	5.7 ± 0.10	17.3 ± 0.59	6.5 ± 0.10	17.8 ± 0.61	7.1 ± 0.15	17.1 ± 0.35	7.6 ± 0.15	18.1 ± 0.41
Distance travelled (m/day)	43 ± 5.9	4 ± 0.3	84 ± 10.6	10 ± 0.6	332 ± 43.5	28 ± 1.6	502 ± 17.0	60 ± 3.9	643 ± 94.6	64 ± 3.1
Feeding rate (g cal/g/day)	150.5 ± 10.49	---	183.7 ± 7.35	---	177.2 ± 16.41	---	197.1 ± 7.06	---	202.6 ± 10.66	---
Absorption rate (g cal/g/day)	143.9 ± 9.61	---	177.4 ± 8.32	---	171.7 ± 15.45	---	189.0 ± 5.65	---	193.0 ± 9.46	---
Conversion rate (g cal/g/day)	+21.9 ± 2.72	−22.8 ± 3.07	+24.7 ± 3.21	−25.8 ± 4.00	+23.7 ± 1.86	−25.4 ± 0.89	+20.4 ± 5.78	−25.3 ± 0.86	+27.4 ± 0.38	−28.6 ± 0.40
Metabolic rate (g cal/g/day)	110.0 ± 7.74	22.8 ± 3.07	137.5 ± 6.38	25.8 ± 4.00	133.2 ± 17.47	25.4 ± 0.89	151.8 ± 6.27	25.3 ± 0.86	149.1 ± 9.60	28.6 ± 0.40
Metabolic rate (ml O_2/g/hr)	0.96 ± 0.07	0.20 ± 0.01	1.21 ± 0.06	0.22 ± 0.01	1.17 ± 0.15	0.22 ± 0.01	1.32 ± 0.05	0.22 ± 0.01	1.30 ± 0.09	0.25 ± 0.01
Absorption efficiency (%)	95.6 ± 0.50	---	96.6 ± 0.95	---	96.8 ± 0.25	---	95.9 ± 0.77	---	95.2 ± 0.38	---
Conversion efficiency (K_2) (%)	15.3 ± 1.45	---	13.9 ± 1.46	---	13.8 ± 2.71	---	10.8 ± 2.94	---	14.2 ± 0.89	---

Previous authors, who worked on the surfacing activity of the air-breathing fishes like *Lepisosteus oculatus* and *Amia calva* generally accept that a raise of temperature increases the frequency (De Roth, 1973; Horn & Riggs, 1973; Saksena, 1975), but they did not consider the possible effects of aquarium depth or feeding (nutritional state) on the surfacing activity.

Hanging

a) Frequency: Data obtained on hanging frequency are given in Tables II to VI and are presented as a function of temperature in the feeding (upper panel) and starving (lower panel) series in Fig. 2; for comparison, the mean hanging frequencies observed for each depth group of either series at the test temperature are indicated by separate symbols. From these data, the following conclusions can be made: 1. Except at 17°C, the feeding series hung
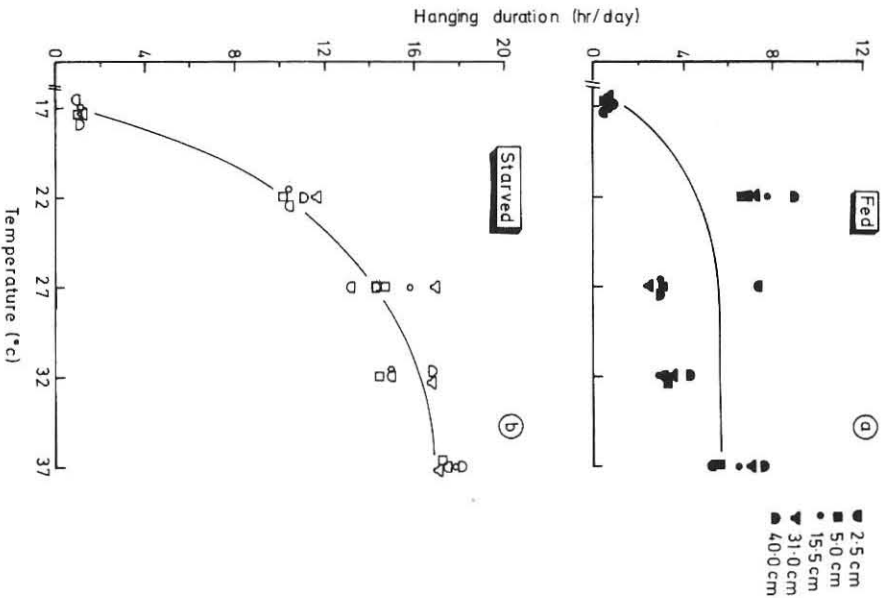

Fig. 3. Effects of temperature and depth of water on hanging duration of the fed and starved *Ophiocephalus striatus*.

Hanging duration (hr/day)

Temperature (°c)

Starved

Fed

● 2·5 cm
● 5·0 cm
● 15·5 cm
◀ 31·0 cm
◀ 40·0 cm

more frequently at any tested temperature than the corresponding starving series, 2. The frequency increased from about 45 time/day at 17°C in either series to about 70 time/day at 37°C for the starving series, and to about 170 time/day at 27 and 32°C for the feeding series, and 3. The frequency is not a depth-dependent behaviour at any tested temperature in either the starving or feeding group.

b) Duration: From an analysis of the data on hanging duration, more or less similar conclusions can be drawn, namely the duration is dependent on temperature as well as on the nutritional state but not always on aquarium depth. For instance, the duration, which was about 0.9 hr/day in either series at 17°C, increased to 6.4 hr/day in the feeding series and to 17.6 hr/day in the starving series at 37°C. Although the duration was not always depth-dependent, maximum differences observed among the different depth groups were statistically significant (e.g. at 27°C, feeding series of 2.5 vs 40 cm; t = 2.492; P < 0.05) at the tested temperatures.

However, comparative analyses of the data on the frequency and duration of hanging suggest that the hanging duration is perhaps an adaptive behaviour to minimize the energy expense on the surfacing activity without involving vertical movement, especially in the starving series. In the feeding series, the frequency is more but the duration per hanging is shorter. For instance, the duration was 1.3 min/hanging for a feeding fish in 2.5 cm aquarium depth at 32°C, as against 9 min/hanging for a starving one; the former hung once in every 13.1 surfacings and the latter once in every 5.4 surfacings. However, calculations of correlation coefficients between surfacing-hanging frequency and surfacing-hanging duration failed to show any definite and significant correlation among the series at the tested temperatures and depths of water (e.g. at 27°C, 40 cm depth, r = 0.998, P < 0.02).

Swimming activity

a) Distance travelled: At all the tested temperatures, the distance swum by the feeding and starving series to exchange atmospheric air was a depth-dependent activity.
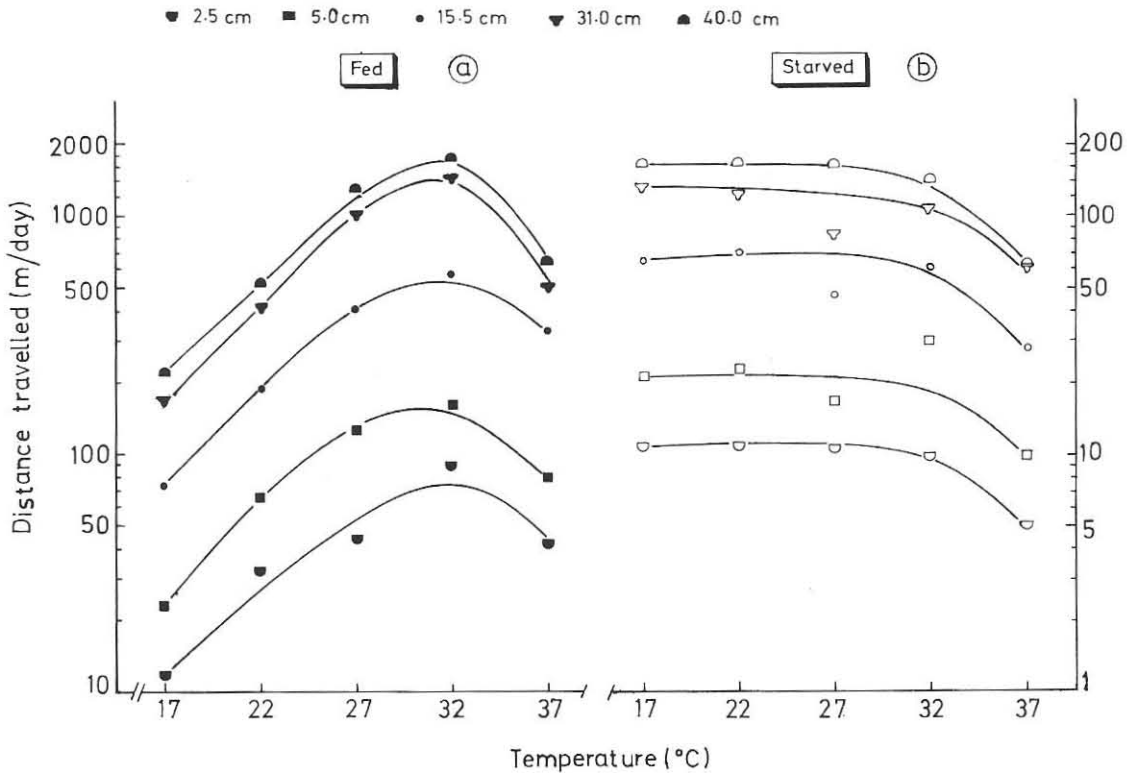

Fig. 4. Semi-logarithmic graph showing the effects of temperature and depth of water on the distance travelled by the fed and starved *Ophiocephalus striatus*.

The longest distance was swum by the feeding series at 32°C and by the starving series at 17°C (Fig. 4). At 37°C, the feeding series reduced the distance not only by decreasing the surfacing frequency (from 2616 time/day at 32°C to 1203 time/day at 37°C in 40 cm aquarium depth), but also by increasing the hanging duration (e.g. from 4.3 hr/day at 32°C to 7.6 hr/day at 37°C). Conversely, the starving series at higher temperatures reduced the distance only by increasing the duration of hanging (e.g. from 1.1 hr/day at 17°C to 18.1 hr/day at 37°C in 40 cm depth). Clearly, the starving series resorts to a behavioural adaptation of hanging to the surface longer as more advantageous than minimizing the surfacing activity.

b) Swimming speed: The feeding series of the 40 cm depth groups steadily increased the swimming speed from 1.2 L (= 4.5 cm)/sec at 17°C to 2.0 L/sec at 32°C, and subsequently decreased to 1.5 L/sec at 37°C (Table VII). But the starving series maintained the speed almost equal (1 L/sec) at all the tested temperatures.

c) Swimming capacity: To estimate the capacity of the fish to swim the maximum distance involved in surfacing activity alone, the maximum time required for the activity by either series exposed to maximum depth (40 cm) as functions of temperature and feeding was calculated and the data are presented in Table VII. The starving series swam for a maximum period of 1 hr/day at 1 L/sec between 17 and 27°C; though the fish maintained the swimming speed, the reduced surfacing frequency (Fig. 1) resulted in the decrease of the total swimming duration to 0.4 hr/day at 37°C. Though the surfacing frequency increased from 219 time at 17°C to 504 time/day at 27°C, the 40 cm depth group of the feeding series maintained not only the distance swum around 165 m/day and the

swimming speed at 1 L/sec, but also controlled the total time spent on swimming activity involved in surfacing precisely at 1 hr/day; this was made possible by increasing the hanging duration from 1.1 hr/day at 17°C to 14.3 hr/day at 27°C. At 37°C, the fish minimized the swimming activity (and the energy expense) not only by reducing the swimming distance involved in surfacing activity but also the time spent on the activity to 0.4 hr/day by increasing the hanging duration to 18.1 hr/day.

The feeding series could afford to spend increasingly longer duration on swimming from 1.1 hr/day at 17°C to 5.4 hr/day at 27°C and subsequently decreased to 1.0 hr/day at 37°C. The feeding series at 37°C reduced the swimming duration by decreasing the number of surfacing, and increasing the hanging duration but not by increasing the swimming speed.

Food utilization
Feeding rate: At all the tested temperatures, the feeding rate of the fish steadily increased with increasing depth (Fig. 5b). The differences in the feeding rates of different groups in each temperature series were statiscally highly significant (e.g. 2.5 vs 40 cm depth at 17°C; t = 17.420, P < 0.001; 2.5 vs 40 cm depth at 37°C: t = 6.945, P < 0.001) and hence the feeding rate is a depth-dependent activity. The mean feeding rate steeply increased (from 33 g cal/g live fish/day at 17°C) with increasing temperature upto 27°C and levelled off (around 200 g cal/g/day) at 32°C and 37°C.

Absorption
a) Efficiency: The efficiency values ranged from 94.3% at 27°C to 97.8% at 17°C; it averaged to 97.2 ± 0.45% (C.V.: 0.5%). The depth and temperature-dependent differences in the efficiency were not statistically significant. This observation supports the previous one, i.e. the efficiency is neither affected by temperature (Davies, 1964; Wallace, 1973) nor by depth of water (Pandian & Vivekanandan, 1976; Arunachalam *et al.*, 1977).

b) Rate: As the efficiency remained more or less equal in all the feeding series (Tables II to VI), the trend obtained for absorption rate as a function of depth or temperature was almost parallel to the respective one obtained for feeding rate vs depth or temperature.

Conversion
a) Efficiency (K_2): Except at 37°C, the efficiency was the highest in the group exposed to the minimum depth at

Table VII. Effect of temperature and feeding on the speed and capacity of swimming the distance involved in surfacing activity of *Ophiocephalus striatus* at 40 cm water depth; each value represents the average performance of 3 to 6 individuals (mean ± SD) observed for a period of 21 to 35 days

| Temperature (°C)		Time interval between two surfacing (sec)	Swimming capacity		Swimming speed (L/sec)
			(sec/surfacing)	(hr/day)	
17	Fed	305 ± 27.8	15 ± 1.4	1.1 ± 0.3	1.2 ± 0.1
	Starved	377 ± 39.0	18 ± 4.3	1.0 ± 0.2	1.0 ± 0.1
22	Fed	81 ± 16.2	13 ± 2.7	2.4 ± 0.5	1.4 ± 0.1
	Starved	222 ± 40.8	18 ± 4.0	1.0 ± 0.3	1.0 ± 0.1
27	Fed	46 ± 9.6	10 ± 3.2	5.4 ± 0.6	1.8 ± 0.1
	Starved	171 ± 35.5	17 ± 1.2	1.0 ± 0.3	1.0 ± 0.1
32	Fed	33 ± 4.3	8 ± 2.6	4.8 ± 0.6	2.0 ± 0.2
	Starved	145 ± 19.3	16 ± 3.7	0.5 ± 0.1	1.1 ± 0.1
37	Fed	72 ± 12.5	12 ± 3.0	1.0 ± 0.1	1.5 ± 0.1
	Starved	265 ± 48.8	17 ± 2.5	0.4 ± 0.1	1.0 ± 0.1
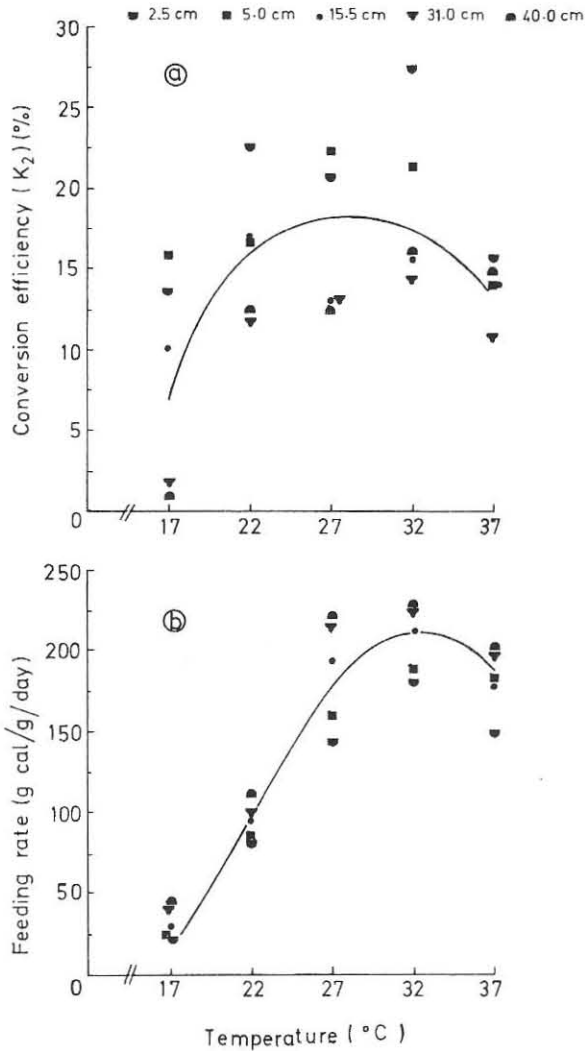
Fig. 5. Effects of temperature and depth of water on feeding rate (b) and conversion efficiency (a) of *Ophiocephalus striatus*. The line in the upper panel showing the relationship between conversion efficiency and temperature is passed through the respective mean values obtained for different depth groups at each temperature series.

the tested temperatures. This depth group consumed the minimum food (Fig. 5b), and still exhibited the maximum efficiency (Fig. 5a), because it perhaps minimized the energy cost of swimming and surfacing activities in the shallowest aquarium (Pandian & Vivekanandan, 1976). Therefore, cultivation of air-breathing fishes like *O. striatus* in shallow waters will be advantageous for two reasons: 1. the high efficiency of food conversion and 2. the low feeding rate.

The mean efficiency was the least (8%) at the lowest temperature of 17°C and moderate (13 to 20%) at the other tested temperatures (Fig. 5a). The maximum conversion efficiency occurred at 32°C, a temperature level, at which different depth groups consumed the maximum ration. Brett *et al.* (1969) showed that the temperate *Oncorhynchus nerka* exhibited the highest efficiency (25%) and consumed about 40 mg dry food/g live fish/day at 11.5°C; the fish converted lower rations more efficiently at lower temperatures than at high temperatures. At lower temperatures (3 to 8°C), the North Sea dab *Limanda limanda* consumed less ration but converted more efficiently (Pandian, 1970). The tropical *O. striatus* converted higher rations more efficiently at high tempera-
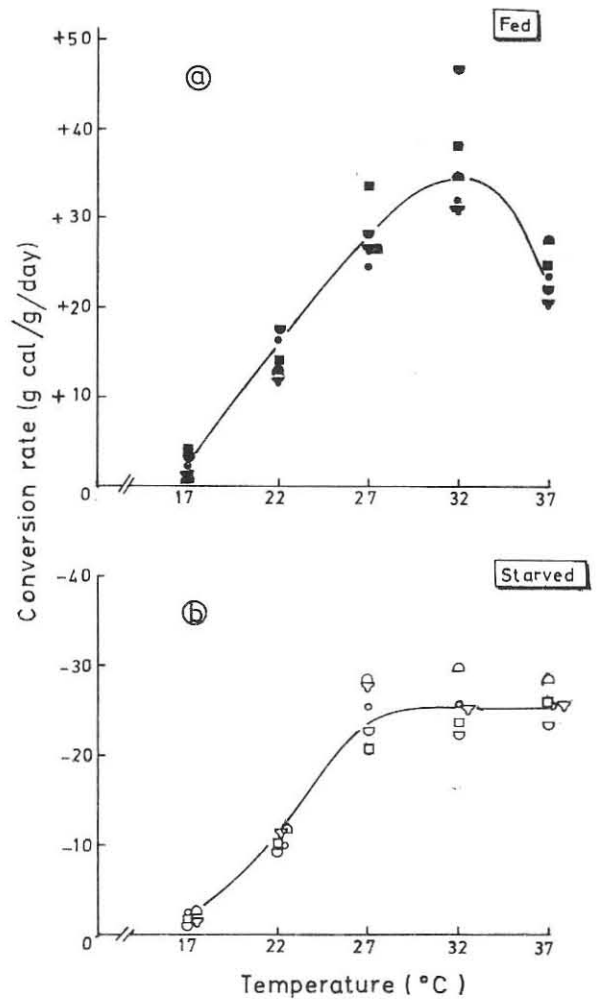

Fig. 6. Effects of temperature and depth of water on the conversion rate of the fed and starved *Ophiocephalus striatus*.

154

tures (22 to 32°C), and the lowest rations with the highest efficiencies at 32°C. Victy Mercy (1967) reported that *O. punctatus* (body weight; 6 g) increased the efficiency from about 6% at lower ration to 22% at higher ration at 27°C. It appears that the lower rations are converted more efficiently by the fishes at temperatures prevailing in their respective natural habitats (see also Averett, 1969; Pandian, 1975).

b) Rate: At 17°C, conversion rate of *O. striatus* was the least (< 4 g cal/g/day) and it steadily increased to the values ranging from 31 to 47 g cal/g/day at 32°C (Fig. 6a) and subsequently decreased to around 24 g cal/g/day at 37°C. At the optimum temperature of 32°C, not only the maximum food is consumed and the highest efficiency is exhibited, but also the highest growth rate is displayed by the fish.

Despite the fact that there was no definite relationship between the depth and conversion rate (see the symbols for the depth groups in Fig. 6a), the differences between the maximum and minimum conversion rates among the depth groups at any tested temperature were significant (e.g. 5 vs 15.5 cm depth at 27°C; t = 2.933, P < 0.05), and in this restricted sense, conversion rate was depth-dependent. The distribution of data presented in Fig. 6a also suggests that conversion is primarily a temperature-dependent and secondarily a depth-dependent 'activity' (see Fry, 1971).

The starving fish, in fact, did not exhibit positive growth activity; however, it converted considerable body substances into metabolic activity. Therefore, the negative growth has been considered as conversion. Conversion rate in the starving series steeply increased from less than 2 g cal/g/day at 17°C to over 25 g cal/g/day at 27°C and levelled off at that level at 32 and 37°C (Fig. 6b). It may be recalled that these starving series at 32 and 37°C hung for longer durations (and also surfaced less frequently at 37°C) and conserved the energy involved in such surfacing and swimming activities. As in the feeding series, a definite relation between depth and conversion rate was not apparent (Fig. 6b); yet the differences between the maximum and minimum rates for any one temperature series was highly significant (e.g. at 32°C, 2.5 vs 40 cm depth t = 10.000, P < 0.001) and again, in a restricted sense, conversion rate is depth-dependent in the starving series also.

Oxygen uptake

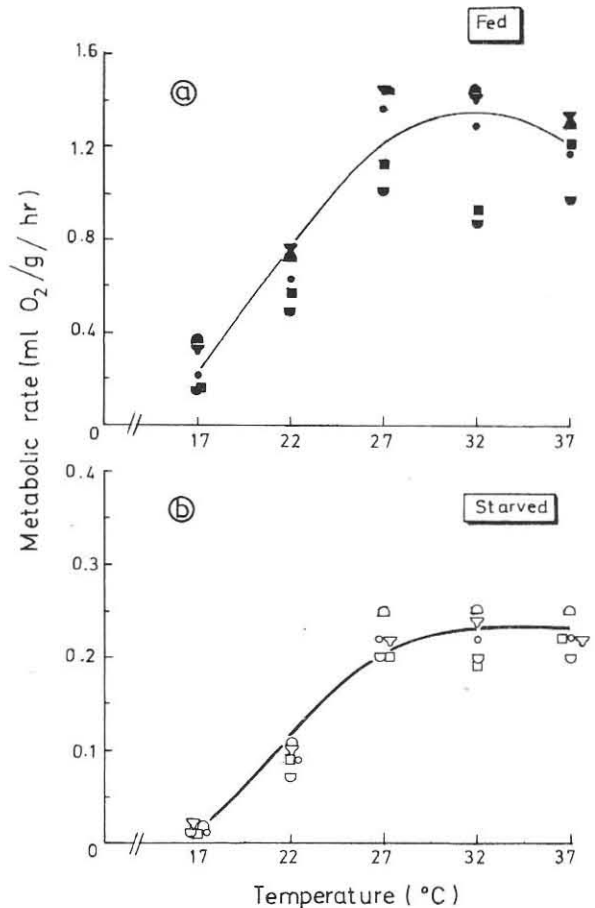The energy equivalent of oxygen uptake of the feeding

Fig. 7. Effects of temperature and depth of water on O_2 uptake of the fed and starved *Ophiocephalus striatus*.

series, which was regarded to have exhibited active metabolism, was less than 0.4 ml/g live fish/hr at 17°C (Table II) and steeply increased to around 1.2 ml/g/hr at 27°C (Table IV) and thereafter levelled off at 32 and 37°C. (Tables V and VI). Brett (1964) also reported that O_2 uptake of active *On. nerka* increased from 0.35 ml O_2/g/hr at 5°C to 0.63 ml O_2/g/hr at 15°C. There was a very significant, and direct relationship between O_2 uptake and depth of water at any tested temperature (Fig. 7; e.g. at 32°C, feeding series of 2.5 vs 40 cm depth, t = 4.798; P < 0.002); hence oxygen uptake is clearly a function of depth of aquarium and temperature. However, O_2 uptake was more dependent on depth at the higher temperatures (> 27°C), while at the lower temperatures (< 27°C), it was predominantly temperature-dependent and the depth played only a secondary role (Fig. 7a). Except for the

absence of a definite relation between the depth groups and O_2 uptake at any temperature (Fig. 7b), the starving series exhibited more or less a similar trend to that of the feeding series.

Discussion

A new design of experiment was employed to collect data on surfacing and swimming activities as well as food utilization as functions of temperature and aquarium depth in the obligatory air-breathing fish *Ophiocephalus striatus*. The swimming activity, speed and capacity measured under the situations in *O. striatus* are far, but not too far from the ones described for the fully gill-breathing fishes like *Oncorhynchus nerka* by Brett (1964, 1970) and *Gadus morhua* by Beamish (1966) and therefore the terms 'swimming activity', 'swimming speed' and 'swimming capacity' used in the present study are not strictly comparable to those of swimming activity and swimming speed described by Brett and swimming endurance by Beamish. Still the present design of experiment, which permitted observations on these aspects of swimming as well as estimations on food utilization on a long term basis, is considered to have also provided a natural habitat for the fish; hence these aspects of swimming are compared with those of other authors to identify common areas of fish metabolism.

O. striatus swam at the maximum speed of 2 L/sec for a period of 8 sec and subsequently rested for an interval of 33 sec; moreover, after every 14 surfacings, the fish also resorted to a behavioural adaptation of hanging to the surfacing for a period of 1.4 min, which involved surfacing without vertical movement. Hence, the maximum period, during which the fish can be expected to perform swimming activity (of course, with interrupted resting periods) at 2 L/sec is 4.8 hr/day. Brett (1964) reported that an active *On. nerka* (10°C; 33 g, 16 cm L) swam at 4 L/sec for a maximum period of about 5 min and became fatigued; the fatigued fish required 3 to 4 hr for recovery. At the time of burst speed, it swam at 10 L/sec for a maximum duration of 20 sec, and then fatigued; the fatigued fish paid off its oxygen debt by deep ventilation during the ensuing 3 to 4 hr recovery period (Brett, 1970). Considering the speed of 4 L/sec for 5 min with the ensuing recovery period of $3\frac{1}{2}$ hr as a cycle, the fish can swim only for a maximum period of about 35 min/day. Beamish (1966) found that swimming at 2 L/sec, *G. morhua* (75 cm L, 600 g) could endure swimming for over 4 hr/day.

O. striatus, enforced to swim longer distance in deeper aquaria at any tested temperature, clearly opted to increase its food intake, and to release more energy from the consumed food for such extra surfacing and swimming activities, rather than to maintain a constant feeding rate and swimming activity, by adjusting the surfacing frequency and/or hanging duration. However, the feeding rate approached an asymptote in deeper aquaria. The aquarium depth, at which the asymptote was reached, progressively shifted from about 40 cm at 17°C to about
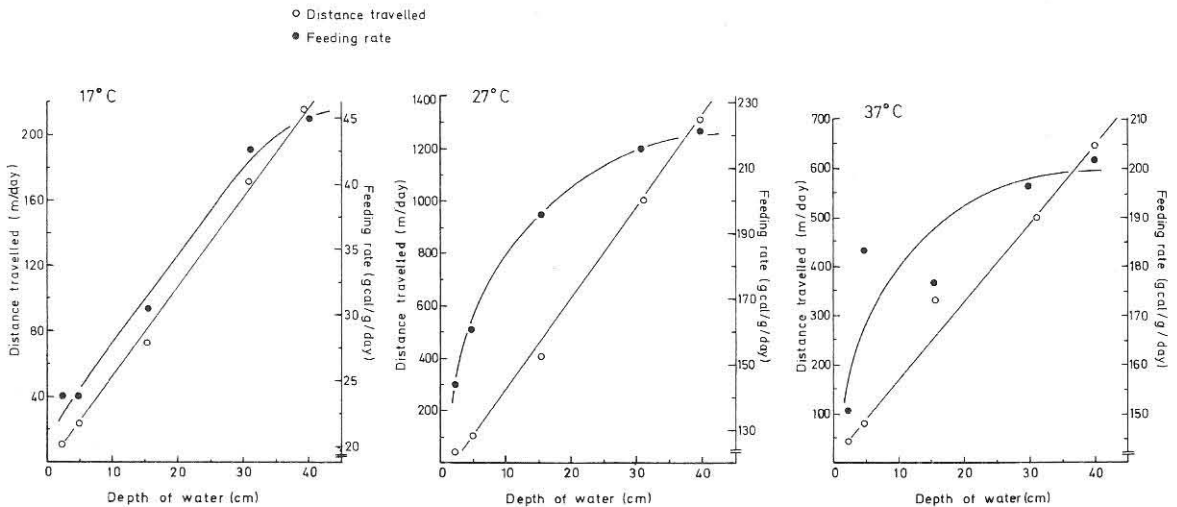

o Distance travelled
• Feeding rate

Fig. 8. Interaction between distance travelled, aquarium depth and feeding rate of *Ophiocephalus striatus* reared at 17, 27 and 37°C.

30 cm at 37°C (Fig. 8). Comparable analyses of the data on O_2 uptake as a function of aquarium depth in the tested temperature series revealed similar trends. But the total distance travelled by the feeding fish continuously increased upto the deepest aquarium (40 cm) and failed to show any inflection. Therefore, the tested aquarium depth did not offer the required opportunity to *O. striatus* to exhibit its maximum swimming performance, although it offered the opportunity to exhibit the maximum rates of feeding and O_2 uptake. This indicates that the fish is perhaps capable of swimming even a longer distance ($>$ 1300 m/day); however, as the trends for food intake and O_2 uptake vs aquarium depth showed an inflection near 30 cm depth, it is evident that the input of food energy and O_2 uptake might have limited the swimming endurance to less than 5.2 hr/day (see also Ware, 1975), had the fish swum longer distance in still deeper aquaria.

When input of food energy became a limiting factor, *O. striatus* reduced the energy cost of swimming by depressing its activity via 1. the decreased surfacing frequency and/or 2. the prolonged hanging duration. For instance, while the fish at 32°C consumed about 225 g cal/g/day at 40 cm aquarium depth, surfaced about 2600 time/day and hung for 4.3 hr/day, that at 37°C consumed only about 200 g cal/g/day, surfaced about 1200 time/day and hung for 7.6 hr/day. Apparently, the surfacing frequency and hanging duration are the two gearing mechanisms available to *O. striatus,* in which swimming activity is likely to be limited by the reduced input of food energy. Though beneficial for survival in the oxygen-deficient waters, the advantageous air-breathing habit and the consequent need for regular surfacing and swimming activities impose a considerable drain of energy, which otherwise could have been channelled into fish production. Therefore, the hanging appears to be an unique adaptive behaviour of *O. striatus,* permitting the fish to surface without involving vertical movement and the consequent energy expense.

The comparability of the minimum maintenance metabolism estimated in the starving *O. striatus* to the standard metabolism of the other fishes, as measured from O_2 uptake, requires qualification. Since standard metabolism is more or less equal to basal metabolism (Brett, 1972), the O_2 uptake must be estimated, when the animal is at complete rest. It should almost be impossible to make the obligatory air-breathing *O. striatus* to rest completely and to estimate basal metabolism. Indeed, it should be equally impossible to make either obligatory or facultative air-breathing fishes, which surface

at regular or irregular interval to exchange atmospheric air, to rest completely and to measure standard metabolism. The O_2 uptake values calculated from the dietary fragment method for the starving *O. striatus* under different experimental conditions range from 0.10 ml O_2/g/hr at 22°C to 0.22 ml O_2/g/hr at 32°C. The values available for the standard metabolism in the literature range from 0.06 ml O_2/g/hr for the starving *Tilapia mossambica* (1 g; 27°C; Pandian & Raghuraman, 1972) to 0.12 ml O_2/g/hr, for *On. nerka* (52 g; 24°C; Brett, 1964). Surprisingly, the minimum maintenance or standard metabolism of the starving of *O. striatus* is nearly 2 to 3 times higher than those reported in the literature. One possibility is that the regular surfacing frequency pushed the standard metabolism up to this high level; however, the energy cost of such swimming activity appears to be partly or fully
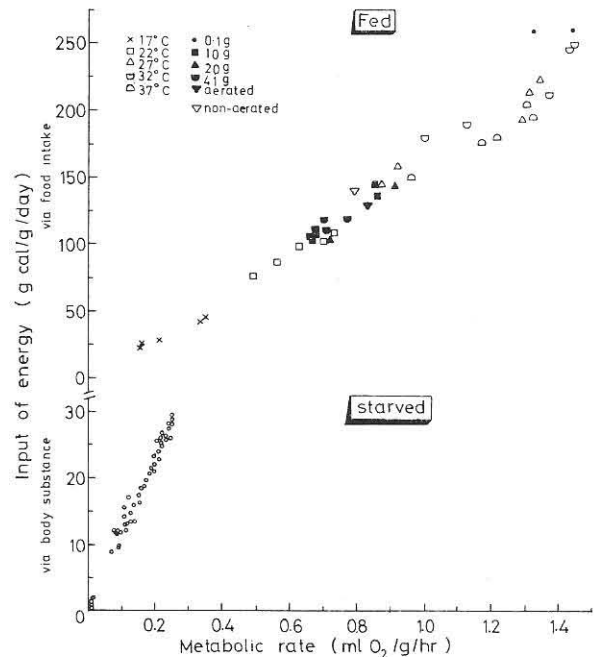

Fig. 9. Relation between input of energy and metabolic rate (O_2 uptake) in the fed and starved *Ophiocephalus striatus* exposed to different temperatures and aquarium depths. Input of energy is represented in terms of food intake, but for the starving one, it is given in terms of body substance metabolized. Corresponding data reported by Vivekanandan (1975, 1976) for *O. striatus* of different weight classes and for those reared under different partial pressure of oxygen are also given for comparison. As the values for the starving fishes fall very close to one another, separate symbols for temperature, body weight and Po_2 series were not given. In the feeding series, the 4 to 5 values given for each temperature and body weight series represent the performance of fishes reared at different aquarium depths.

compensated by the facts that fully gill-breathing fishes must ventilate larger volume of water than the air-breathing fishes at similar O_2 uptakes and that the greater energy cost of aquatic breathing is further aggravated by the huge density difference between the two media; in brief, air-breathing is advantageous in terms of O_2 availability (Johansen, 1970).

Barring the series reared at 17°C, the active metabolic level of *O. striatus* was 5 to 7 times higher than the respective standard metabolic level; briefly, the highest O_2 uptake value obtained for *O. striatus* in the deepest aquaria was 1.44 ml/g/hr at 32°C and to the best of our knowledge, this is the highest O_2 uptake value known for fishes. The highest O_2 uptake values available in the Russian literature are 0.9 ml/g/hr for the sturgeon fry (23 mg) *Acipenser guildenstaedt,* 0.95 ml/g/hr for the carp fry (110 mg) *Cyprinus carpio* and 0.75 ml/g/hr for (160 mg) *Ac. stellatus* (see Winberg, 1956). It is not clear from Winberg (1956) whether these estimations were made in completely starving fishes, and if so, these low values may not represent the active metabolism. The highest O_2 uptake value estimated in the present study may be considered as the maximum sustained activity metabolic level (Brett, 1972) and compared with the one (0.63 ml O_2/g/hr) reported for *On. nerka* (50 g) at 15°C (Brett, 1964). Brett's value is one of the highest values vailable in the English literature; but it is less than half of that assessed for *O. striatus*. The possible reasons for this discrepancy have been discussed in detail elsewhere (Vivekanandan, 1975; Pandian & Vivekanandan, 1976).

Although much information have been accumulated on the effects of the PO_2 and PCO_2 of water and air on the surfacing frequency and the proportion of oxygen obtained from water and air (Carter, 1957; Hughes & Shelton, 1962; Saxena, 1963; Qasim *et al.,* 1966; Johansen, 1970; Steen, 1970), no paper relates the surfacing frequency to the total metabolic level of an air-breathing fish. Fig. 9 shows direct and good correlations between rate of food/fish energy input and O_2 uptake in the feeding and starving *O. striatus* as functions of ration, aquarium depth, PO_2, temperature and body weight. Incidentally, the almost vertical trend obtained for the O_2 uptake vs rate of fish energy input reveals the remarkable ability of the starving fish to economize its metabolic expenses. Therefore, the data obtained in the present study on the behavioural activities associated with air-breathing habit, namely, surfacing, hanging and swimming have been correlated with the respective O_2 uptake for the series tested different aquarium depths and temperatures in Fig. 10, from which the following conclusions may be drawn:

1. With increasing O_2 uptake, the surfacing frequency and swimming activity increased more or less linearly, and hanging duration decreased. An exception is the series at 17°C, which consumed less than 0.4 ml O_2/g/hr and still hung only for about 1 hr/day, although they were expected to hang for 12 hr/day (Fig. 10b). A second exception is the series at 37°C, which exhibited 'S' shaped trends for the O_2 uptake-swimming distance relationship (Fig. 10c & d) and 2. In all cases, the values obtained for
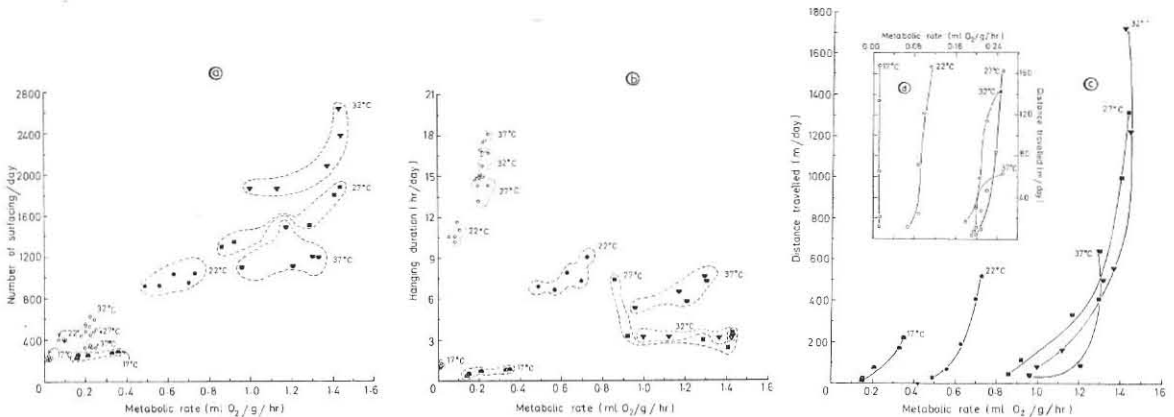

Fig. 10. Metabolic rate as functions of surfacing frequency (panel a) and hanging duration (panel b) in the feeding (represented in closed symbols) and starving (represented in open symbols) *Ophiocephalus striatus* reared at different temperature levels. The relationships between metabolic rate and distance travelled in the fed and starved *O. striatus* reared at different temperatures are given in panels c and d. For each temperature, the 5 values represent the performance of fishes tested at different aquarium depths.

the starving fish exposed to different temperatures and depths of aquarium fell closely in the left corner of the graph and those of the feeding series occupied a greater area in the right side. This clearly shows that feeding elevates O_2 uptake, and the O_2 uptake, in turn, triggers off frequent surfacing, which results in greater swimming activity.

For want of comparable literature on temperature effects on food utilization in the tropical fishes, a discussion on the results obtained on the effects of temperature on food utilization of *O. striatus* has not been made.

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