Food intake, absorption and conversion in the fish *Ophiocephalus striatus*[1]

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KURZFASSUNG: **Nahrungsaufnahme, Absorption und Konversion bei dem Fisch *Ophiocephalus striatus*.** Individuen von *Ophiocephalus striatus* BLOCH wurden nach verschieden langen Hungerzeiten gefüttert, um Aufschlüsse über Aufnahme, Absorption und Konversion der Nahrung zu erhalten. Nach einer Hungerperiode von weniger als 20 Tagen nahm die Nahrungsaufnahme um das Dreifache zu. Hungerten die Tiere länger als 20 Tage, so steigerte sich die Nahrungsaufnahme hingegen nur geringfügig. Trotz der erhöhten Nahrungsaufnahme war der Absorptions-Nutzeffekt dem der Kontrolltiere gleich. Der Konversions-Nutzeffekt verdoppelte sich bei Individuen, die weniger als 20 Tage gehungert hatten; daraus resultierte eine „Überkompensation" des Wachstums. Bei Tieren, die nach einer Hungerperiode von mehr als 20 Tagen wieder gefüttert wurden, konnte eine gewisse Verringerung des Konversions-Nutzeffektes sowie eine teilweise Kompensation festgestellt werden. Diese Ergebnisse werden im Hinblick auf ähnliche Versuche bei *Esox lucius* (IVLEV 1939) diskutiert. Es wird die Schlußfolgerung gezogen, daß sich bei Fischen, die nach verschieden langen Hungerzeiten erneut gefüttert werden, zwei Typen unterscheiden lassen: beim ersten Typ ist die Nahrungsaufnahme geringer als vor der Hungerzeit, der Konversions-Nutzeffekt jedoch durch Erniedrigung der für den Stoffwechsel aufgebrachten Energie erhöht; beim zweiten Typ erreichen Nahrungsaufnahme und Stoffwechselintensität sofort die Werte vor der Hungerzeit oder übertreffen diese sogar. Hierbei wird die Erhöhung der Nahrungsaufnahme von einer entsprechenden Vergrößerung des Konversions-Nutzeffektes begleitet.

INTRODUCTION

Partial or complete starvation during winter in temperate fish (RICKER 1946) and during summer in tropical fish (NIKOLKSY 1963) is followed by normal or voracious feeding and subsequent restoration of growth during the ensuing more favourable season. In spite of the importance of such metabolic adjustments, this aspect of nutritional physiology has remained a virgin field; the few observations scattered in the literature (MORQULIS 1919, IVLEV 1939, 1961, MOORE 1941) give a confused picture. The present work has been undertaken with the view to throw some light on this interesting aspect.

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MATERIAL AND METHODS

The fish *Ophiocephalus striatus* BLOCH (Ophiocephalidae) represents the test organism for the present study, and the prawn *Metapenaeus monoceros* (living but immobilized by a cut on the dorsal side between cephalothorax and abdomen) served as its food. Both were collected and maintained in the laboratory as described by PANDIAN (1966). The fish or prawn to be subjected to chemical analyses was dried to constant weight, homogenized and preserved. Faecal matter was collected once every 7 to 10 days by filtering the entire aquarium water. From these samples, aliquots were taken for estimation of nitrogen and calorific contents. Total nitrogen was determined following the standard procedure of STEYERMARK (1951). Calorific contents were estimated by the moist combustion method originally described by IVLEV (1935). All experiments were conducted at a water temperature of $28^0 \pm 1.5^0$ C.

EXPERIMENTAL DESIGN

A total of 10 fishes of similar size and nutritional history were used; all were kept individually in single aquaria. They were subdivided into two series: (1) an experimental series and (2) a sample series. From the sample series, one fish was removed after 0 day, 10 days, 20 days, 30 days and 40 days of starvation respectively, and subsequently analysed for nitrogen and calorific contents. Correspondingly, in the experimental series one fish was removed after 0 day, 10 days, 20 days, 30 days and 40 days; these were immediately transferred to feeding aquaria where they were fed ad libitum with prawn for exactly as many days as they had been starved. The "0 day" individual underwent no starvation period but continuously received food for a period of 20 days. At the termination of the experimental feeding, test fish were killed for nitrogen and calorific estimations. The difference between the nitrogen and calorific contents of the sample fish and experimentally fed ones represented the quantity of nitrogen and energy retained by the fish during the experimental feeding period. This procedure is similar to the "sacrifice method" described by MAYNARD & LOOSLI (1956).

RESULTS

Food intake

Each day the fish of the experimental series were allowed to feed for a period of 10 to 12 minutes. From the amount of food consumed, the average feeding rate was calculated for each fish. The daily food intake amounted to 2.7 % body weight (unless qualified the term body weight indicates wet weight) for the "0 day" individual, 8.1 and 7.0 % body weight for the ones fed after 10 and 20 days starvation, respectively (Fig. 1). Subsequently, rate of feeding decreased to 3.9 and 4.8 % body weight for the individuals fed after 30 and 40 days fasting, respectively. A period of less than

20 days fasting increased feeding 2 to 3 times, a period of more than 20 days 0.5 to 0.8 times above the normal feeding level.

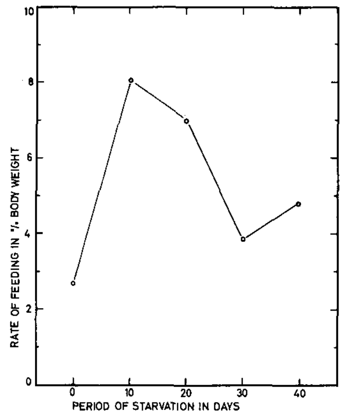

Fig. 1: Feeding rate in the fish *Ophiocephalus striatus* fed with an unlimited supply of immobilised prawn *Metapenaeus monoceros*. The fish were fed following different periods of starvation

The lower feeding rate in the individuals fed after a 30 or 40 day period of fasting (and subsequently fed over equally long periods of time) is due to the intake of less food during the last days of the feeding period rather than during the days immediately after fasting. After 30 days fasting, the experimental fish consumed on an average 5.6 % body weight of food/day for the first 10-day-period, 2.5 for the second and 3.5 % body weight/day for the third 10-day-period (Table 1). The corresponding

Table 1

Changes in the recovery feeding rate of the fish *Ophiocephalus striatus* during different periods of feeding following varying periods of starvation. The fish were fed with prawn for exactly as many days as they had starved previously

Weight of fish (g)	Fish fed after fasting for	Recovery feeding rate (% body weight/day) during entire period	I 10-day period	II 10-day period	III 10-day period	IV 10-day period
35.09	0 day	2.70	—	—	—	—
21.99	10 days	8.09	8.09	—	—	—
37.57	20 days	7.01	7.23	6.79	—	—
33.14	30 days	3.86	5.58	2.49	3.52	—
25.10	40 days	4.83	5.10	6.15	4.70	3.50

values for 40-day experimental fish were 5.1, 6.2, 4.7 and 3.5 % body weight/day for the first, second, third and fourth 10-day-periods, respectively. The 20-day experimental fish yielded 7.2 and 6.8 % body weight/day for the first and second 10-day-periods. Thus the effect of starvation on the feeding rate depends on the duration or the length of fasting. On resumption of feeding after a period of starvation, feeding rate is increased; the magnitude of such an increase depends on the length of the starvation period. Further, the effect of such increase persisted only for a few days immediately following starvation and later decreased.

Absorption

The quantity of food absorbed was estimated by subtracting the quantity of faeces evacuated from that of food consumed. Since chitin present in the exoskeleton of prawn is not digestible (Mann 1948, Gerking 1952, Pandian 1966), its nitrogen and calorific contents have been substracted from those of food consumed, and faeces (for details consult Pandian 1966). Absorption efficiency was determined relating the net nitrogen and calorific contents of food absorbed to those consumed. The values

Table 2

Absorption and conversion efficiencies of protein and food in *Ophiocephalus striatus* fed following different periods of starvation. The fish were fed prawn exactly as many days as they had starved previously

Fish fed after fasting for	Absorption efficiency		Conversion efficiency	
	Protein (%)	Food (%)	Protein (%)	Food (%)
0 day	95.83	89.78	16.25	26.02
10 days	96.85	93.74	44.34	47.99
20 days	96.47	92.21	43.10	51.11
30 days	95.74	85.70	22.49	38.61
40 days	96.23	87.48	28.76	36.97

obtained for nitrogen absorption efficiency varied from 95.7 to 96.9 % (Table 2); they did not differ appreciably from those obtained for the controls (95.8 %). However, there was a slight decrease in total food absorption efficiency in fish fed following a period of more than 20 days fasting; it was about 92 % in those fed after 10 and 20 days fasting and decreased to 85.7 % and 87.5 % in those fed after 30 and 40 days fasting (Table 2), respectively.

Conversion

The quantity of nitrogen and energy retained by the fishes fed for different periods was estimated. In the experimental series, the average amounts of nutrient matter consumed, absorbed and converted per day were calculated and are presented in Tables 3 and 4. Conversion efficiency was very high in experimental individuals after 10 and 20 days fasting (Table 2). It was about 44 % for nitrogen and 50 % for total food in these fishes (Fig. 2). The efficiency decreased to about 25 % for nitrogen conversion and to 37 % for total food conversion in fish fed after a period of more than 20 days fasting.

Table 3

Total nitrogen balance of *Ophiocephalus striatus* fed with prawn following different periods of starvation

Fish fed after fasting for	N consumed (mg/day)	N in faeces (mg/day)	N absorbed (mg/day)	N converted (mg/day)	N residual (mg/day)
0 day	29.94	1.26	28.68	4.75	23.91
10 days	54.54	1.72	52.82	23.42	29.40
20 days	81.00	2.82	78.18	33.70	44.48
30 days	39.43	1.95	37.48	8.43	29.05
40 days	37.32	1.40	35.92	10.33	25.59

Table 4

Total energy balance of *Ophiocephalus striatus* fed with prawn following different periods of starvation

Fish fed after fasting for	Food consumed (Cal/day)	Food in faeces (Cal/day)	Food absorbed (Cal/day)	Food converted (Cal/day)	Food residual (Cal/day)
0 day	1.044	0.106	0.938	0.244	0.694
10 days	1.676	0.105	1.571	0.754	0.817
20 days	2.490	0.194	2.294	1.174	1.121
30 days	1.212	0.174	1.038	0.301	0.737
40 days	1.148	0.144	1.004	0.371	0.633

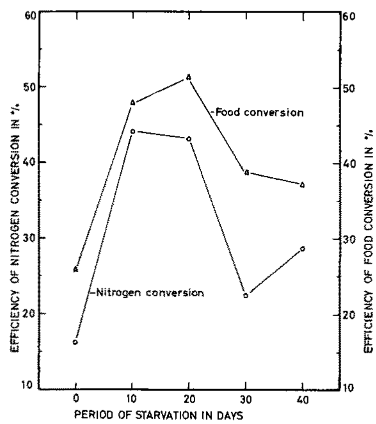

Fig. 2: Efficiencies of nitrogen and food conversion in *Ophiocephalus striatus* fed with unrestricted supply of prawn. The fish were fed following different periods of starvation

Since conversion of food into body tissue of fish results in growth, the quantity of food converted by those individuals resuming feeding after varying periods of starvation has a bearing on compensatory growth. The "0 day" fish converted 0.244 Cal energy for growth per day (Table 4). At this rate, it can be expected to convert about

4.880 Cal energy for growth over a period of 20 days. A fish fed for 10 days after a period of 10 days fasting, if it is to completely recover or compensate its growth, can be expected to convert at the rate of 0.488 Cal for growth per day. 20, 30, and 40-day-experimental fishes may be expected to convert with similar efficiencies during the corresponding periods. The rate of energy conversion was more than double in individuals fed after a period of less than 20 days fasting (Table 4). Such increased conversion rate is termed "over-compensation" (Wilson & Osbourn 1960). Fishes fed after a period of more than 20 days starvation showed only partial compensation.

DISCUSSION

Rate of food intake increased 2 to 3 times in O. *striatus* fed after less than 20 days fasting; a period of more than 20 days fasting led to a much less pronounced increase: 0.5 to 0.8 times the normal. This observation supports the results obtained on *Esox lucius* by Ivlev (1961). In O. *striatus*, increased feeding rates persisted only for a few days after resumption of feeding and later decreased during the last days of the recovery-feeding period. Observations of mammalian physiologists show increase of appetite and food intake and their subsequent decrease in rats fed after a period of starvation (Wilson & Osbourn 1960). These authors have suggested that starvation somehow stimulates the nerve centers controlling appetite and that the response to such a stimulation does not persist for a longer period.

My observations on absorption have two limitations: (1) they are based on very few experiments and (2) the possibility of bacteria destroying the faecal matter in aquaria for 7 to 10 days, particularly at the high temperature of 28° C. The second limitation appears to be not too significant in view of Davies's (1964) observations, who has shown that bacterial destruction of faecal matter of the carp *Carassius* at 21.5° C over a period of 14 days was negligible. Smith's (1935) data on protein nitrogen absorption efficiency of the lung fish *Protopterus aethiopicus* fed after 32 and 40 days starvation do not show any appreciable differences from those of regularly fed ones. Morqulis (1919) studied efficiency of protein nitrogen in trout fed after varying periods of starvation. His data show that absorption efficiency ranged from 90 to 95 %; this is in agreement with the present results. However, Morqulis noted that fat absorption efficiency decreased in trout fed after a fasting period. While nitrogen absorption efficiency remained uniform, efficiency to absorb total food decreased in O. *striatus* fed after more than 20 days fasting. In view of Morqulis's (1919) observation, decrease in efficiency of total food absorption in O. *striatus* may possibly be due to lower fat absorption efficiency. Morqulis assumed that prolonged starvation may damage lipase-secreting glands in the pancreas and intestine of the fish.

The interesting point is that fishes fed after less than 20 days fasting were feeding at very high rates (7 to 8 % body weight/day) and yet were able to absorb the nutrient matter as efficiently as the one fed regularly (2.7 % body weight/day). Thus conversion efficiency is a function of feeding rate. It has been reported that the fish fed with restricted food supply exhibited a better efficiency than the other fed with unrestricted food supply. This has been shown for example in *Cyprinodon macularius* by Kinne

(1960). Other authors, like HUNT (1960), reported that there was a definite, but not proportionate increase in the digestion rate in *Lepisosteus platyrhincus* at higher levels of feeding. GERKING (1955) and PANDIAN (1966) fed fishes at different rates and reported that there were no appreciable differences in their ability to absorb protein. DAVIES (1964) fed carp *Carassius auratus* of about 35 g size from 1.5 to 38 mg dry weight of food/g fish/day and observed no marked difference in their energy extraction efficiency. It may be concluded therefore that with increasing feeding rates, the rates of digestion and absorption tend to increase up to a certain level of optimum and thereafter they are reduced again.

My results obtained for conversion efficiency are in agreement with those obtained by IVLEV (1939) using *Esox lucius* in that a period of less than 20 days fasting increased efficiency of food conversion. But there are notable differences in details. IVLEV's data for food intake show a progressive decrease from 3.780 Cal/day for fish fed regularly to 2.348 Cal/day for the fish fed after 20 days starvation (Fig. 3). For the corresponding nutritional state in *O. striatus*, the quantity of food consumed increased from 1.044 Cal/day to 2.490 Cal/day (Fig. 4). Although intake of food decreased in *E. lucius* fed after less than 20 days fasting, it is said that "the energy consumed is more adequately utilized" (IVLEV 1939, p. 91) by correspondingly reducing the energy expended on metabolic processes. In *O. striatus*, increase in conversion efficiency was due to increase in rate of food intake. The reason why efficiency of food conversion in *E. lucius* declined after a prolonged period of fasting has been attributed to "the serious upsetting

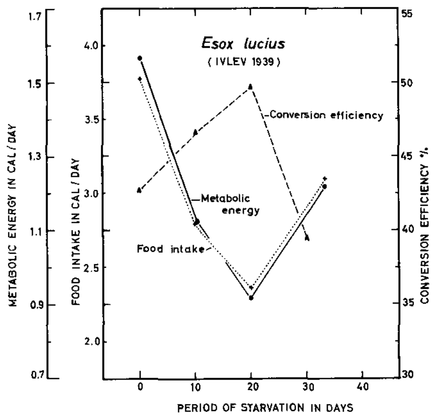

Fig. 3

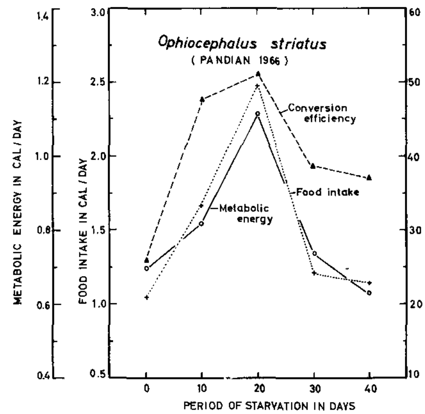

Fig. 4

Figs. 3 and 4: Effects of different periods of starvation on transformation of food and metabolic rates of *Esox lucius* and *Ophiocephalus striatus*

of the process of digestion" (IVLEV 1939, p. 92). For corresponding nutritional states, *O. striatus* showed equally good efficiencies of absorption as those of regularly fed fish, the less pronounced increase in conversion efficiency in them was due to relatively lower increase in food intake (Figs. 3 and 4).

IVLEV's (1939) data show that resumption of feeding in *E. lucius* at any one period varying from 10 to 30 days did neither restore feeding nor metabolism to the pre-starvation rate. I have no direct data on metabolism of O. *striatus*, but the quantity of energy available for metabolism (FRY 1947) has been calculated (see residual N and residual food in Tables 3 and 4) by subtracting the energy converted for growth from that absorbed. In O. *striatus*, resumption of feeding at any one period, immediately restores feeding and metabolism to a slightly higher than normal, pre-starvation rate in fish fed following a period of 30 and 40 days fasting, and to a still higher degree in those fed after 10 and 20 days fasting. SMITH (1935) followed respiration of unfed *Protopterus aethiopicus* over a period of 600 days at 25° C. He observed that feeding at any one time during this period of 600 days, tends to immediately restore metabolic rates to pre-starvation level. RAFFY's (1933) experiments on gold fish and young eels display the same phenomenon. Therefore, it appears that responses to resumption of feeding after various periods of fasting may be of two types: (1) feeding is not restored to the pre-starvation rate but conversion efficiency is increased by a decrease in energy expended on metabolism. e.g., *Esox lucius* (IVLEV 1939); (2) upon resumption of feeding, food intake as well as metabolic rate are restored immediately to their pre-starvation rates or to even higher levels; the magnitude of such elevation in feeding rate being accompanied by a corresponding increase in conversion efficiency, e.g., O. *striatus* (Figures 3 and 4).

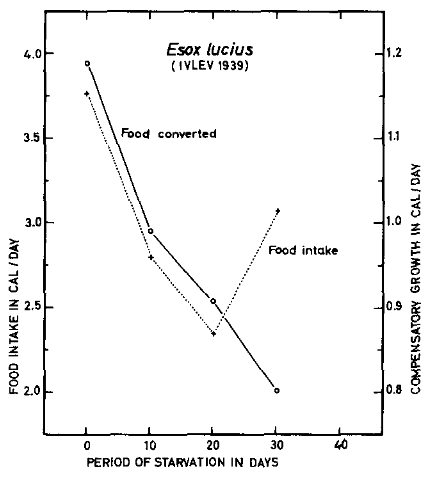

Fig. 5

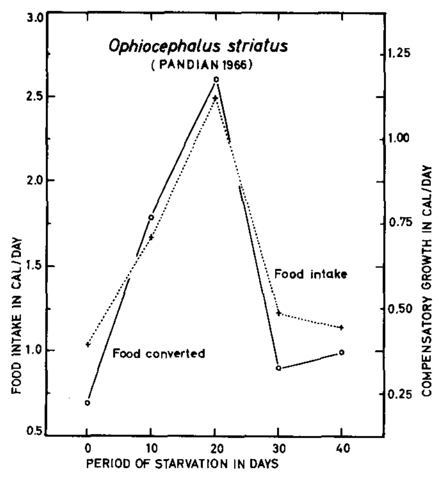

Fig. 6

Figs. 5 and 6: Effect of starvation on food intake and compensatory growth in *Esox lucius* and *Ophiocephalus striatus*

The quantity of nutrient matter converted by O. *striatus* fed following different periods of starvation was always greater than that of the controls and showed partial or over-compensatory growth (Fig. 6). When the corresponding data obtained for *E. lucius* are plotted, it is seen that in spite of the higher efficiency, conversion rate was considerably lower (Fig. 5). As can be seen from Figures 5 and 6, the degree of compensatory growth depends on the feeding capacity of the fish.

SUMMARY

1. In the fish *Ophiocephalus striatus* BLOCH feeding rate increased 2 to 3 times, when feeding was resumed after less than 20 days fasting; fasting periods of more than 20 days result in resumption-feeding rates that were only slightly higher (0.5 to 0.8 times) than the controls.
2. Although feeding rates were very high after resumption of feeding following different periods of starvation (10 to 40 days) absorption efficiency remained practically identical to that of controls.
3. Following a period of less than 20 days fasting resumption of feeding led conversion efficiencies almost twice as high as the normal values, showing "overcompensation". Fish fed after a period of more than 20 days fasting showed a decrease in conversion efficiency resulting in partial compensatory growth.
4. Responses to resumption of feeding following different periods of starvation may be of two types: (a) Rates of metabolism and feeding are restored to pre-starvation rates and conversion efficiency increases due to corresponding increase in feeding rates, e. g. *O. striatus,* and (b) rates of metabolism and feeding continue to remain low and the increase in conversion efficiency is due to a corresponding decrease in energy expended on metabolism e. g., *E. lucius.*

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Discussion following the paper by PANDIAN

PAFFENHÖFFER: Bacterial action may influence the dissolved organic excrements to a greater extent than the particulate faeces.

PANDIAN: This may be true. I have concentrated only on the protein and energy contained in the filterable particulate faecal matter. As I have pointed out, DAVIES (1964) has demonstrated that the quantity of particulate faecal matter destroyed by bacterial action during the period of 14 days at 21.5° C is negligible.

PAFFENHÖFFER: Did the conversion efficiency and feeding rate of *Ophiocephalus striatus* obtained after the different periods of starvation stay at the same level throughout the following life stages or did they level off?

PANDIAN: Presumably you refer to such changes in irreversible nongenetic adaptation as have been reported by KINNE in *Cyprinodon macularius (Comp. Biochem. Physiol.* 5, 265, 1962). I have not made such long term experiments. The longest duration of my experiment was 40 day feeding following a period of 40 day starvation. As you see in Table 2, food intake during the first 10-day-period of the recovery feeding was 5.4 % body weight/day i.e. 189 % of the control fish. It gradually levelled off to 120 % (3.5 % body weight/day) during the fourth 10 day period of the recovery feeding. I am therefore inclined to say that the high feeding rate and conversion efficiency observed after different periods of starvation will gradually level off in the following life stages.

SAVAGE: Did you notice any significant changes in the activity of the fish either during or after starvation experiments?

PANDIAN: In a preliminary experiment, in which 5 individuals were kept starving in an aquarium, they were observed to be active, chasing each other incessantly and eventually became cannibalistic biting the tail of others. In fact it is for this reason that my experiments had to be based on single fish. Such "hunting behaviour" was observed in the starving individuals till about 15 to 20 days. Those starved for more than 20 days were resting motionless in the corner of the aquarium. At the end of 40 days starvation, the fish was very much emaciated with deeply sunken eyes.

KRÜGER: Haben Sie die Fische bis zum Tode hungern lassen? Wenn es so ist, haben Sie die Bestimmungen über die Zusammensetzung des Körpers durchgeführt?

PANDIAN: Ich habe keine derartigen Untersuchungen durchgeführt. Sie finden Angaben darüber bei SMITH (1939a, b) und IVLEV (1961). Ich wollte wissen, wie sich Stoffwechselrate und -nutzeffekt im Hinblick auf Ernährung und Konversion verändern, sobald die Tiere sich an die Nahrungsaufnahme nach verschiedenen Hungerperioden angepaßt haben. Bezüglich der chemischen Zusammensetzung der hungernden Fische beobachtete ich eine deutliche Abnahme des Energiegehaltes (11 % in Cal/g Trockengewicht) und eine Zunahme des Wassergehaltes (4 %).