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ENERGY COSTS AT DIFFERENT LEVELS OF FEEDING IN JUVENILE COD

by

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ABSTRACT

As part of a wider study of the energy budget of free-living juvenile cod, we have used an open system respirometer to determine the costs of food utilisation for captive fish at different levels of feeding.

Prior to the study, fish were acclimated to the experimental temperatures (7, 10, 15 and 18°C), kept under natural light conditions, and fed inside the respirometer. During the experiment, fish were fed on a special formulated diet of similar composition to their natural diet, at different levels and their oxygen consumption monitored for a 11-15 day period.

After feeding, the rate of oxygen consumption increased to well above the pre-feeding level, usually 8-12 hours after feeding, and thereafter declined gradually. The maximum increase in rate of oxygen consumption was observed usually at the end of the feeding period (8th day).

The energy expenditure as measured by oxygen consumption was highly dependent upon ration size. For fish fed to satiation, the energy expenditure was 12.9, 14.92, 16.14 and 21.47% of the ingested energy at 7°, 10°, 15° and 18° respectively.

RÉSUMÉ

Comme contribution à une étude plus étendue du budget d'énergie des morues juvéniles vivant en liberté, nous avons employé un compteur de respiration à système ouvert pour déterminer la consommation d'énergie de l'utilisation de la nourriture pour des poissons en captivité à des niveaux différents d'alimentation.

Avant l'étude les poissons ont été acclimatés aux températures des expériences (7, 10, 15 et 18°C); on les a gardés dans des conditions d'éclairage naturel et ils ont été alimentés à l'intérieur du compteur de respiration. Pendant l'expérience on a alimenté les poissons selon un régime spécial qui serait semblable à leur régime naturel à des niveaux divers, et on a surveillé de consommation d'oxygène pour une période de 13 à 15 jours.

Après l'alimentation, le taux de la consommation d'oxygène s'est augmenté à un niveau bien plus élevé qu'avant en générale de 10 à 15 heures après l'alimentation et après cela, il est tombé par degrés. L'augmentation maximum du taux de la consommation d'oxygène a été observée en générale à la fin de la période d'alimentation (8 ième jour).

La dépense d'énergie selon la consommation d'oxygéne a été déterminée en grande partie par les quantités d'alimentation. Dans le cas des poissons alimentés jusqu' à satiété, la dépense d'énergie était 12.9, 14.92, 16.14 et 21.47% de l'énergie inérée à 7°, 10°, 15° et 18°C respectivement.

INTRODUCTION

As part of a study of the physiological energetics of free-living juvenile cod, Gadus morhua, we have looked at various factors affecting the metabolism of the fish under laboratory conditions. In particular, we have looked at the metabolic costs of food processing by the fish.

It is now clear that ingestion of food by animals results in an increase in their rate of oxygen consumption and is accompanied by heat production. The increased energy expenditure associated with feeding can be attributed to:

1. Excited feeding behaviour, with increased locomotor and other activities.
2. The mastication and digestion of food taken into the gut.
3. The biochemical transformation of the absorbed food material, formerly termed the Specific Dynamic Action (SDA). The component especially involved protein metabolism, but also includes the release of energy accompanying lipid and carbohydrate metabolism.

Where the distinction is not made between the various above mentioned factors, the term "apparent SDA" has been applied to the whole increase in metabolic rate associated with feeding (Beamish, 1974).

Little comparative information is available on the actual energy cost of food utilisation of apparent SDA for different species. Notable exceptions are the measurements made by Brody (1945) on cattle; Muir and Niimi (1972) on a fish, the aholehole, Kullia sandvicensis; the work of Beamish (1974) on largemouth bass, Micropterus salmoides; and Brett and Zala (1975) on sockeye salmon, Oncorhynchus nerka.

Warren and Davis (1967) concluded that the energy freed and lost through protein catabolism (which they supposed was the principal part of specific dynamic action) and other digestive processes ranged from 5 to 40% of the ingested food energy for fish. Pierce and Wissing (1974), recorded the energy cost of food utilisation as being between 4.8 to 24.4% of the caloric content of the daily food intake in the bluegill, Lepomis macrochirus. Recently, Vahl and Davenport (1979) reported an SDA cost of 10% of the ingested energy in the blenny, Blennius pholis. Thus, it seems that the energy expended during the ingestion, digestion, absorption and assimilation of food material may comprise a significant part of total respiration.

In the present study we have investigated the energy cost of food utilisation in juvenile cod at four different temperatures (7°, 10°, 15° and 18°C) by monitoring the oxygen consumption of fish under different feeding regimes. We have calculated the contribution of the energy expended in food utilisation to the total energy budget of cod at several levels of feeding.

MATERIALS AND METHODS

Preliminary preparation

Cod were caught with hand lines in Loch Torridon, a sea loch on the west coast of Scotland. They were then transported to the Marine Laboratory, Aberdeen and were kept in large rectangular tanks, (6" x 4" x 3" deep). Prior to the experiment, fish were acclimated to the appropriate experimental temperatures (7°, 10°, 15° and 18°C) by daily changes of one degree and then held at these temperatures for at least 4 weeks. The fish were kept under subdued light conditions with a maximum intensity of 10 $W.sr^{-1}.m^{-2}$ at the surface. This intensity was chosen to approximate the light intensity during summer daytime at a depth of 10 metres in Loch Torridon.

A multichannel dissolved oxygen meter allowed five individual experiments to be run simultaneously at each temperature. These five fish were fed at different levels, keeping each in a separate open circuit respirometer.

The respirometer

Metabolic rates were determined in open circuit respirometers. The individual respirometers were simply made from perspex cake containers (23 x 23 x 11 cm^3) with an outflow and inflow built in (Figure 1). A hole, 50 mm diameter, was drilled in the top of the container to allow feeding during the experiment. The aperture was resealed after each meal. The respirometers were connected to a common aerated seawater supply from a header tank at a height of 1.5 metres. To keep the temperature constant the respirometers were placed in a common water bath.

The rate of flow through each respirometer was adjusted so that the metabolism of the fish did not reduce the ambient oxygen level below 75 - 80% of the air saturation level. The rate of flow was maintained constant by the adjustment of two valves on the outflow of each respirometer.

The oxygen concentration of the inflowing water was measured in the header tank, and maintained at air saturation level. The oxygen concentration at the outflow was measured for each respirometer by a polarographic oxygen electrode (Orbisphere, model 2104, connected to Orbisphere, multichannel oxygen meter, model 2710). The output from each electrode was recorded on a data logger (Solartron, type 3430BD) giving print-outs at half hour intervals.

At each temperature, a control respirometer without a fish was used to see if there was any decrease in oxygen level due to diffusion of oxygen from the rubber tubing and other fittings, or resulting from the growth of algae or bacteria in the respirometer.

Feeding

During the experiments fish were fed on a specially formulated diet made up in pellet form. The different ration levels were matched to a given percentage of wet body weight, measured at the start of each experiment. Five feeding levels were chosen as tabulated in Table 1, and were termed "starved", "below maintenance", "maintenance", "above maintenance", and "satiation".

Experiment Number		Fish Numbers 1 below maint.	2 maint.	3 above maint.	4 satiation	5 starved
1	Fish weight (g)	82.90	36.6	61.41	60.85	59.0
	Ration as % wet body weight	1.03	1.37	1.94	3.67	0.0
2	Fish weight (g)	41.2	45.6	50.0	42.4	61.3
	Ration as % wet body weight	1.53	1.75	1.79	3.73	0.0
3	Fish weight (g)	20.3	46.2	54.3	51.2	39.4
	Ration as % wet body weight	2.03	3.0	3.41	5.14	0.0
4	Fish weight (g)	74.3	60.0	40.6	61.0	56.1
	Ration as % wet body weight	1.35	2.6	3.64	5.21	0.0

TABLE 1 Fish weight (g) and food intake (% wet body weight) for each fish at each experimental temperature.

The chosen levels were calculated from the unpublished results of a growth experiment where the growth rates of cod were studied in relation to ration size. The growth rate (g/day) was plotted against food intake and the intercept of the regression line on food axis was taken as the maintenance ration required by the fish. Other appropriate levels of feeding were also determined from this regression line. For the fish fed to satiation an unlimited quantity of food was offered at each feeding until the animal refused to take any more.

The components of the diet were similar to those making up the natural diet of the juvenile cod in the wild at Loch Torridon and consisted of crustaceans, polychaetes, molluscs and fish. The proportions of each different food item were determined by taking the percentage of the food items found in the stomachs of wild fish and weighting these by an experimentally determined digestion coefficient for each item. The materials were mixed together with a binder, macerated, freeze-dried, converted into moist pellets and kept in a deep freeze until presented to the fish.

The caloric content of the diet was determined with a Phillipson microbomb calorimeter (Phillipson, 1964). The value was 5.61 Kcals/g or 23.49 KJ/g ash free dry weight.

Biochemical analyses showed that protein and lipid were the main components of the diet.

Fish were fed every two days on a pre-weighed quantity of pellets, and the feeding period lasted 8 days in each experiment. To feed the fish, the lod of the respirometer was opened and food was offered, then the lid was carefully replaced and sealed so that no air bubbles were trapped inside the respirometer. The starved or unfed fish were treated in an identical manner, except that food was not offered.

Experimental procedure

At each experimental temperature five fish were examined, the metabolic rates of each individual fish being determined in the following sequence. The fish, acclimated to the experimental temperature, was first anaesthetised with a solution of benzocaine (ethyl-p-amino benzoic acid) and its length and weight measured to the nearest 0.5 cm and 0.1 g respectively. After recovering from the anaesthetic the fish was placed in the respirometer. At this stage the fish was nearly always excited and showed a high oxygen consumption. The fish was then allowed to adjust to the respirometer for 3 or 4 days before the actual experiment started. After this period of adjustment the steady level of oxygen consumption of the unexcited and undisturbed fish was determined and taken as the pre-feeding level to compare with the fed fish. The oxygen consumption determined under these condition is known as the routine metabolism (Fry, 1957).

When the fish showed no further major changes in oxygen consumption, the lid was removed, the appropriate amount of food offered to the fish in the respirometer and the lid then replaced. Extra care was taken to minimise disturbance to the fish during feeding. The fish usually took the full quantity offered, but if any was rejected it was removed and weighed before the lid was replaced. This quantity was then subtracted from the total quantity offered.

The oxygen levels were thereafter monitored at 30 minute intervals. Temperature was recorded simultaneously and the atmospheric pressure measured 3 times daily. The rate of flow of water through each experiment was measured every 8 hours. The differences in oxygen level between inflow and outflow together with the rate of flow through the respirometer, the atmospheric pressure, the salinity and the weight of the fish, was used to calculate the rate of oxygen consumption per kg live weight per hour.

After the final measurement, the fish was weighed and the mean weight during the experiment determined for further calculation. The experiments were conducted for 11 to 15 days. From the composition of the diet, an oxycalorific equivalent of 4:63 Kcals per litre of oxygen was applied to convert the oxygen consumption of the fish to the energy consumption. The difference in average metabolic rate between the pre-feeding state and the feeding state was used to calculate the energy costs of food utilisation and the contribution of this component to the energy budget.

RESULTS

Increase in oxygen consumption following feeding

The rate of oxygen consumption of the cod increased after the first meal, reaching a peak some hours later. The rate of rise and the level reached depended upon ration size and was larger for more substantial meals. When the same fish received a second meal two days later the oxygen consumption had still not fallen to the pre-feeding level, and following receipt of the second meal the oxygen consumption increased to a new peak, generally higher than the first. The maximum oxygen consumption was usually observed towards the end of the third or fourth meal.

Measurements taken on a single fish (69.8 g) fed to satiation at 10°C for a long series of meals showed that oxygen consumption reached its maximum after the third meal, and thereafter remained at or near this level as feeding continued (Figure 2). On this basis, we believe that four meals fed over eight days allow oxygen consumption to reach its maximum.

The fish showed a decline in oxygen consumption when feeding stopped, but in most cases observations did not continue for long enough for definite conclusions to be drawn about the actual time taken for oxygen consumption to drop to the pre-feeding level. In general, the rate of oxygen consumption took several (3-4) days to decline significantly but the rate of decline depended on both ration size and temperature. The decline was slower for larger meals and lower temperatures.

The increase in oxygen consumption following feeding depended upon ration size and temperature as illustrated by the data in Table 2 which shows the mean and peak metabolic rate of the fish reached during the feeding period expressed as a percentage of the pre-feeding level for five different ration levels and four different temperatures.

Figures 3 to 6 illustrate the changes in oxygen consumption for fish fed at different ration levels at different temperatures of 7°, 10°, 15° and 18°C. In these figures the mean oxygen consumption of fish over 24 hours is plotted against time. The cumulative effect of the consecutive meals upon oxygen consumption is clearly demonstrated.

Dependance of oxygen consumption upon ration size

The percentage increase in oxygen consumption was greater at higher feeding levels. The Wilcoxen paired sample test (Zar, 1974) was applied to the data to test for differences in O_2 consumption at the different ration levels at a given temperature. This showed significant differences $p < 0.001$ between all fish maintained at the same temperature except for two fish, fed at maintenance and above maintenance ration at 7°C, where no significant difference could be shown.

The increase in mean oxygen consumption (expressed as a percentage of the mean pre-feeding level) is plotted against ration size in Figure 7. Regression analysis showed a significant relationship between ration size and percentage increase in oxygen consumption at all temperatures, and levels of significance increased as the temperature increased. The regression coefficient, elevation and F value at each temperature are given in Table 3.

The mean rate of oxygen consumption (mg kg^{-1} h^{-1}) against ration size (expressed as a percentage of body weight) at several temperatures is shown in Figure 8. There was a linear relationship between the rate of oxygen consumption and ration size at all temperatures. Regression analysis showed that the association between rate of oxygen consumption and ration size is significant for all temperatures, the level of significance increasing with temperature. The regression coefficient, elevation and F value at each temperature are given in Table 4.

The effects of temperature

Temperature clearly affected the magnitude of the increase in oxygen consumption following feeding. Comparison of the slopes and elevations of the regression equations for percentage increase in oxygen consumption against ration size (given in Table 3) showed that the slopes of the

TABLE 2 Metabolic Rates Associated with Different Levels of Feeding

Temperature	feeding level	metabolic rates (mg of O_2/kg/hr) mean prefeeding level	mean during feeding	% increase from prefeeding level	peak	% increase from prefeeding level
7°C	below m.	101.61 ± 16.70	102.89 ± 15.43	1.26	118.50 ± 22.51	16.62
	maintenance	86.82 ± 3.53	135.42 ± 42.37	55.98	172.14 ± 51.80	98.27
	above m.	95.67 ± 21.67	135.30 ± 24.62	41.42	161.98 ± 12.55	69.31
	satiation	87.71 ± 18.36	167.59 ± 38.25	91.10	201.95 ± 29.08	130.25
10°C	below m.	130.14 ± 14.92	152.43 ± 17.08	17.13	165.32 ± 17.22	27.03
	maintenance	155.31 ± 43.98	168.14 ± 16.08	8.26	180.74 ± 24.28	16.37
	above m.	124.91 ± 23.08	178.03 ± 26.84	42.53	194.42 ± 36.03	55.65
	satiation	122.20 ± 20	201.15 ± 33.75	64.61	226.31 ± 47.37	85.20
15°C	below m.	176.29 ± 15.32	223.62 ± 25.35	26.85	253.03 ± 15.00	43.53
	maintenance	171.36 ± 23.85	227.87 ± 27.82	32.98	254.43 ± 24.55	48.48
	above m.	140.76 ± 9.54	243.27 ± 34.65	72.82	279.01 ± 26.07	98.22
	satiation	161.40 ± 9.89	318.94 ± 63.10	97.61	384.80 ± 18.13	138.41
18°C	below m.	150.33 ± 16.58	180.19 ± 28.83	19.86	193.32 ± 45.95	28.60
	maintenance	157.70 ± 16.91	223.49 ± 32.71	41.71	260.37 ± 14.37	65.10
	above m.	150.10 ± 16.84	279.80 ± 59.31	86.41	341.57 ± 38.19	127.56
	satiation	143.60 ± 29.91	308.15 ± 57.82	114.83	353.92 ± 49.77	143.46

regression lines for all temperatures did not differ significantly from each other except for 15° against 18°C. The elevation accounted for the differences in all non-neighbouring temperatures but did not differ significantly for neighbouring temperatures.

Comparison of the regression equations for rate of oxygen consumption against ration size shows significant differences in the slopes of the equations for all temperatures, except for 7/10°C and 15/18°C.

To demonstrate the effect of temperature upon oxygen consumption at different feeding levels we have corrected the ration size to a constant percentage of body weight. The oxygen consumption for the corrected ration was calculated from the appropriate regression equations (Table 4), and then plotted against temperature (Figure 9). The results show that for a ration of fixed size (in terms of percentage of wet body weight) the rate of oxygen consumption increased with temperature, reaching a maximum at 15°C, and tending to decrease above this temperature. An exception was the data for the above maintenance level of feeding, where oxygen consumption was still greater at 18°C.

The energy expended in food utilisation

To calculate the energy expenditure associated with feeding at different ration levels and different temperatures the rates of oxygen consumption were converted to their caloric equivalents, and then expressed as a percentage of the energy of the ingested food. The values are given in Table 5.

Except for data at maintenance level for 7°C and 10°C there is an increase in the energy cost with ration size. The data for maintenance ration at 7°C is affected by the very low pre-feeding level of oxygen consumption by this individual fish, and by a peak in oxygen consumption after the second feeding, perhaps reflecting increased excitability. Together, these factors gave a rather large percentage increase in the oxygen consumption. Similarly, the data for maintenance ration at 10°C is affected by a very high pre-feeding level of oxygen consumption, giving a rather small percentage increase in oxygen consumption with feeding.

Taken as a whole, the data provide strong evidence for an increase in the energy cost of food utilisation with ration size. The data also indicating that the costs of food utilisation increase with temperature. The greatest cost, (22% of the ingested energy) is consumed by fish on large rations at 18°C.

Discussion

It is well established that in fish, as in other vertebrates, the oxygen consumption increases following the ingestion of food (Brody, 1945; Averett, 1969; Muir and Niimi, 1972; Pierce and Wissing, 1974; Beamish, 1974; and Vahle and Davenport, 1979). The magnitude of this increase is dependent on both ration size and the environmental temperature. This phenomenon, often termed apparent SDA, has usually been measured as the increase in the rate of oxygen consumption after a single meal.

We have found that rise in oxygen consumption is rather slow, so that with consecutive feeding the effect is cumulative and the maximum oxygen consumption generally appears after several meals. Thus, the maximum oxygen consumption attributable to apparent SDA will depend very much on the feeding regime that is followed. If we consider a fish like the cod as a continuous predator, it is most appropriate to accept the mean oxygen consumption measured during a prolonged period of feeding as the actual oxygen consumption attributable to food utilisation, as done during this study (Figure 2).

Saunders (1963), Beamish (1974) and Vahle and Davenport (1979) reported that oxygen consumption takes 2-4 hours to reach to its maximum level after feeding. Our own observations showed that it took a much longer period (usually 8-12 hours) to reach a peak for cod, at our study temperatures. This discrepancy may reflect the presentation of a more rapidly assimilated diet by other workers, or a higher temperature. However, it is possible that in some cases the rapid build-up could be due to an increased excitability of the fish following feeding rather than to the digestion and assimilation of food. Digestion rates measured for cod (Jones, 1974 and Hawkins, unpublished data) indicate that it takes a very long time for food to be eliminated from the stomach. Slow build-up of oxygen consumption after feeding in our experiments almost certainly reflects their very slow digestion rate. No attempts were made to measure the energy costs arising from excitability of cod in our experimental conditions. However, our results from starved fish, which showed in some cases very small increases during the mock feeding period (1.89 and 0.45% of pre-feeding level for starved fish at 7° and 15°C respectively). We have therefore concluded that the costs of increased excitability of fish in our experiments are small and that the main increase in oxygen consumption after feeding can be attributed to food utilisation (apparent SDA).

Although the experiments did not continue for long enough to allow any definite conclusion to be drawn about the actual time required for oxygen consumption to drop to the pre-feeding level, in general the rate of oxygen consumption decreased to the pre-feeding level within a few days of the last meal. The rate of decline was both ration and temperature dependant. This results are consistent with those of Beamish (1974) and Vahle and Davenport (1979). Saunders (1963) in a study on the effect of feeding on the metabolic rate of Atlantic cod (wt 1 kg), at 10°C, reported that the routine metabolic rates of starving fish rose from 75 to 112 mg of O_2/kg/hr after feeding and remained at this elevated level for 1 to 2 days, falling gradually back to the fasting, routine rate by the seventh day.

The most comprehensive study of apparent SDA was made by Averett (1969) on young coho salmon, Oncorhynchus kisutch. Under conditions of varying ration and temperature, heat increments ranging from 3.4 to 45% of the energy ingested were reported, with most values pronounced between 9 and 15% ("Heat increment" is a term which has been used by some workers, for example, Rubner, 1902; and Averett, 1969 to express the increase in metabolic rate after feeding).

Muir and Niimi (1972) determined SDA for two specimens of aholehole for which they obtained a value of 16% of the ingested energy of rations of tuna flesh at two ration levels (2.3 and 4.5% weight). The study by Smith (1973) on the sluggish sargassum fish, Histrio histrio, (1 and 28 g) fed to satiation level, resulted in a range of heat increments from 15.2 to 36.2%, the overall average being 23.7% of the ingested food

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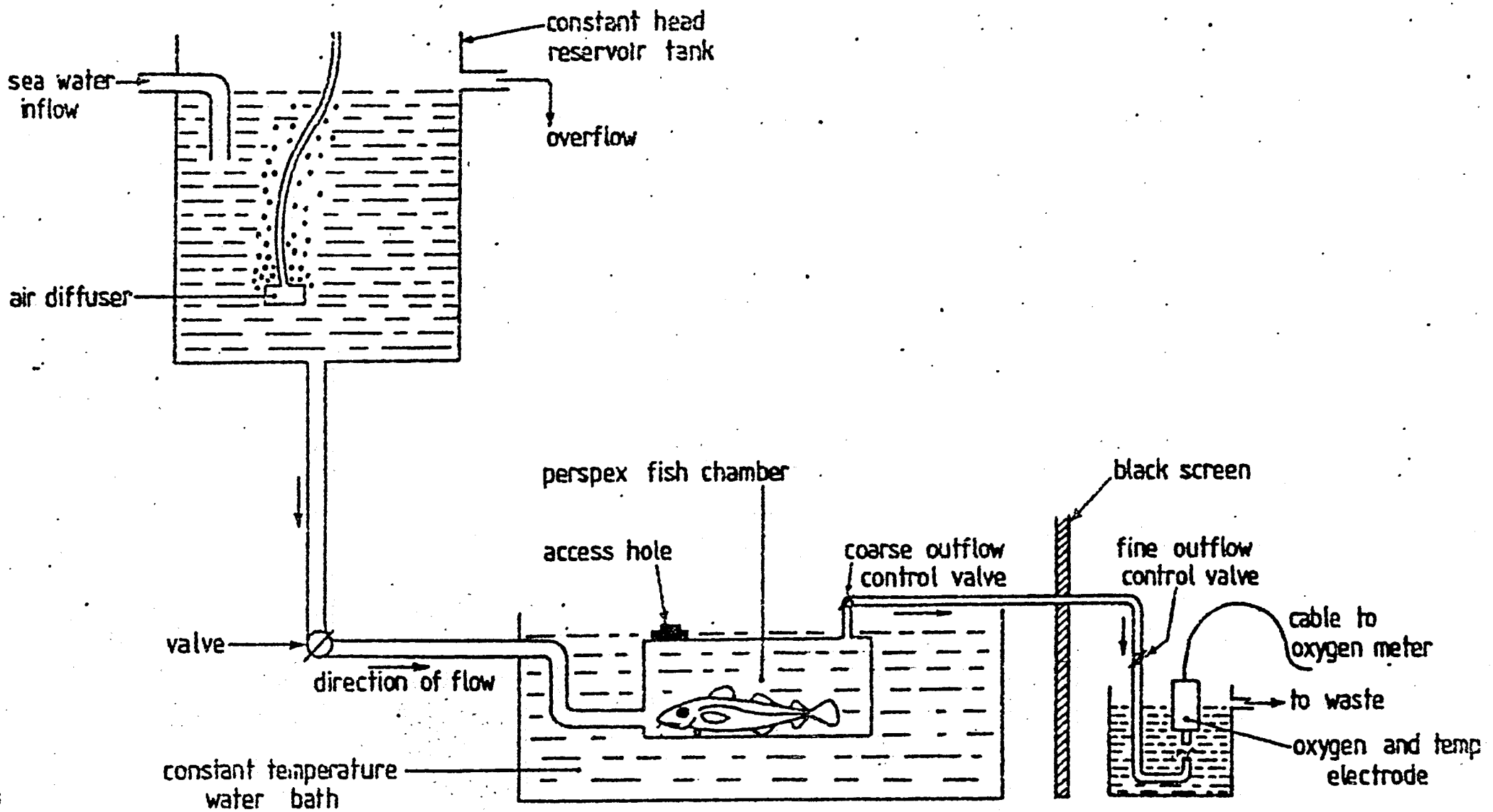

Figure 1 Diagram of the respirometer used for the determination of oxygen consumption.

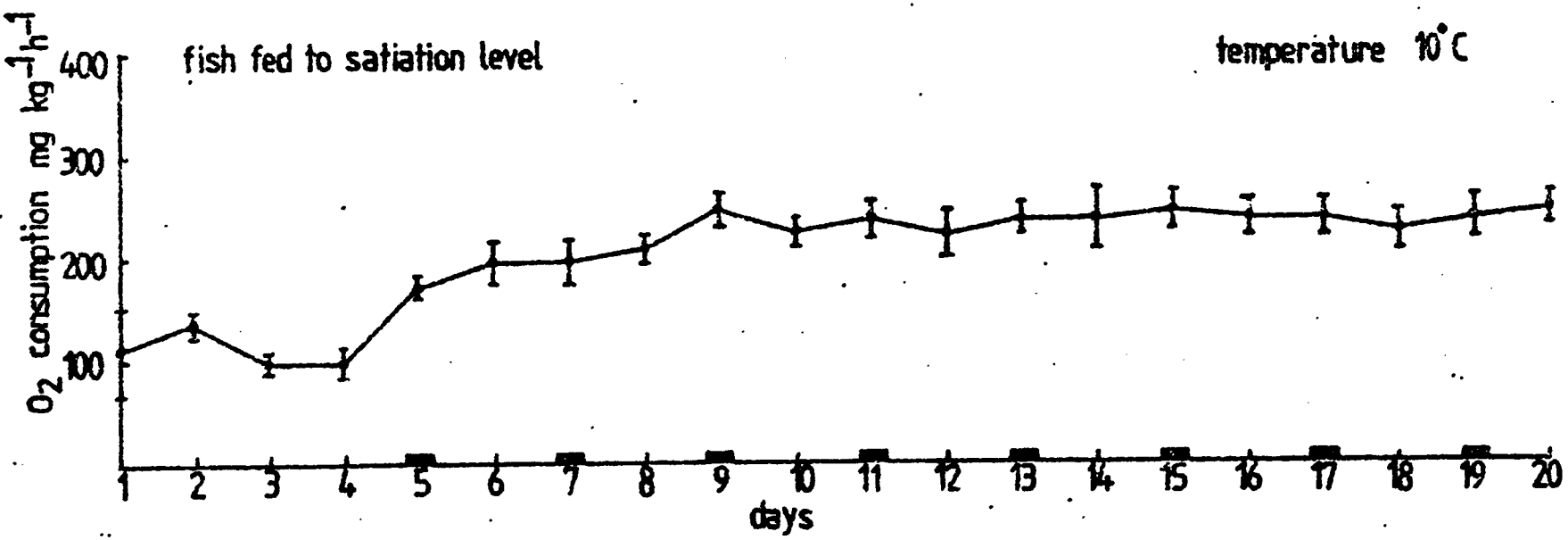

Figure 2 Oxygen consumption of a single fish with time where each point is a mean reading taken over 24 hours. Days on which the fish were fed are blacked

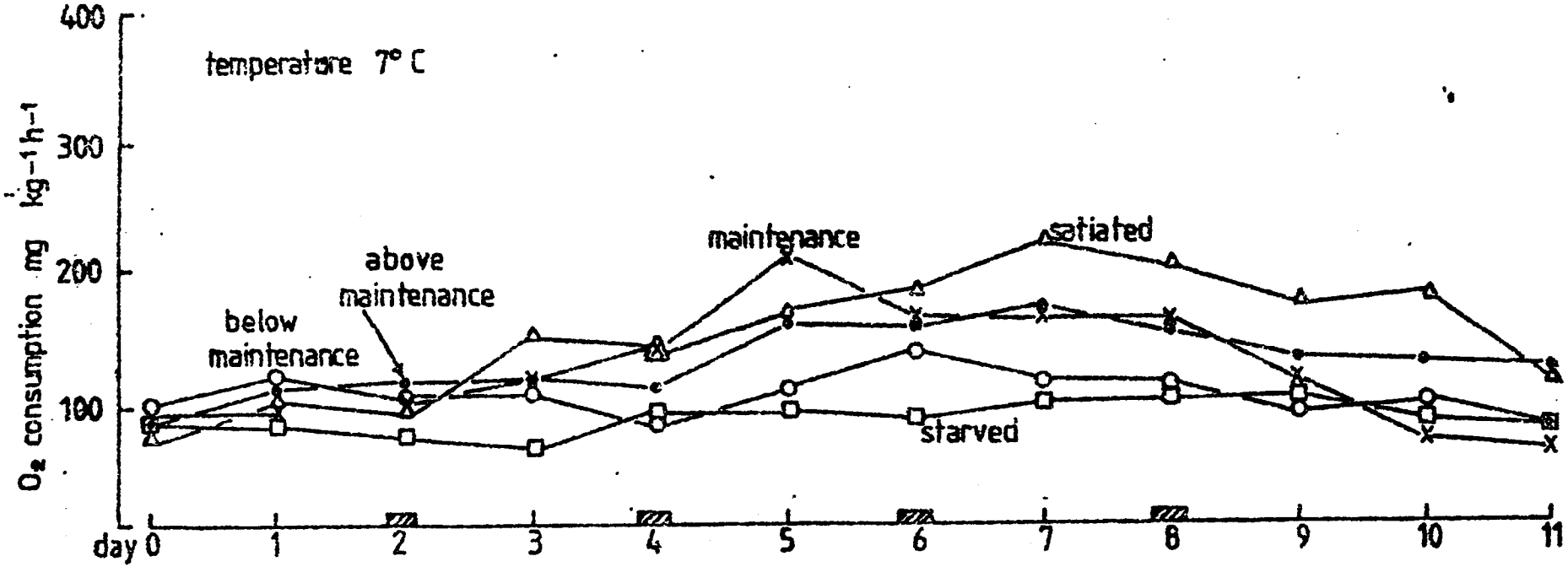

Figure 3 Oxygen consumption of a single fish with time where each point is a mean reading taken over 24 hours. Days on which the fish were fed are hatched

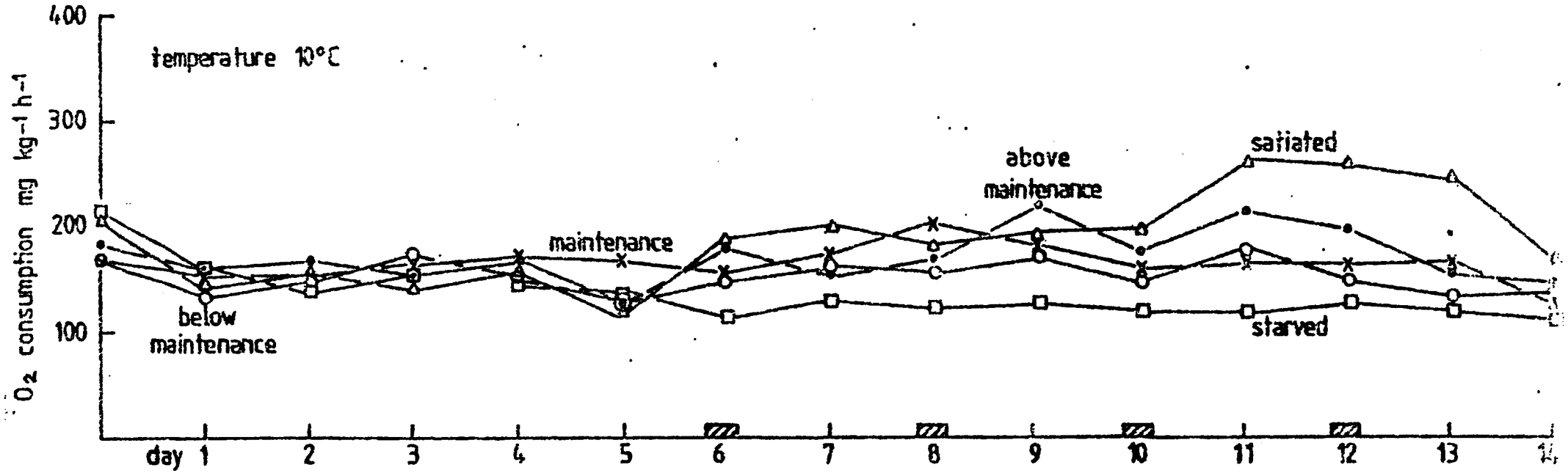

Figure 4 Oxygen consumption of fish with time where each point is a mean reading taken over 24 hours. Days on which the fish were fed are hatched.

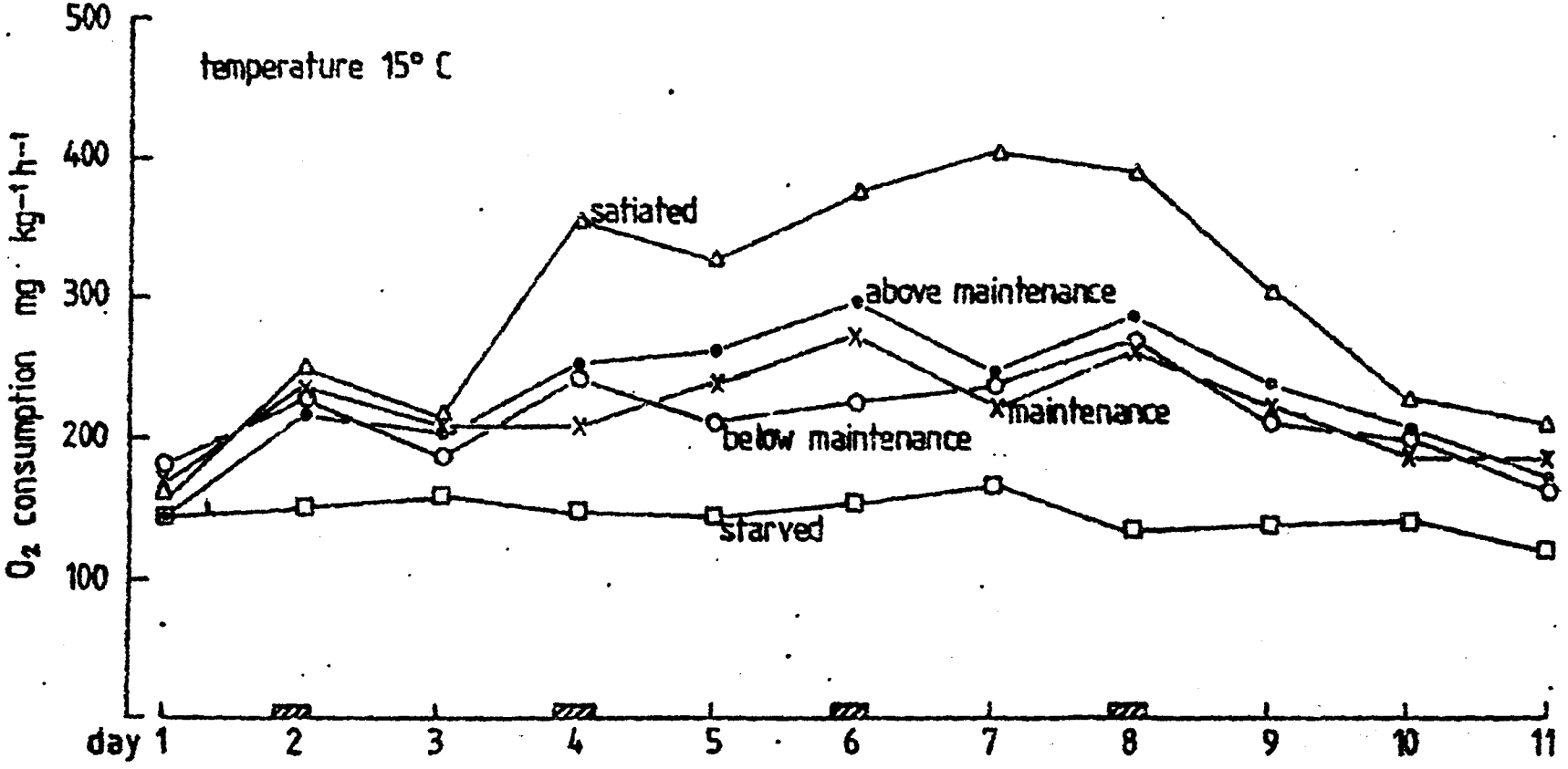

Figure 5 Oxygen consumption of a single fish with time where each point is a mean reading taken over 24 hours. Days on which the fish were fed are hatched

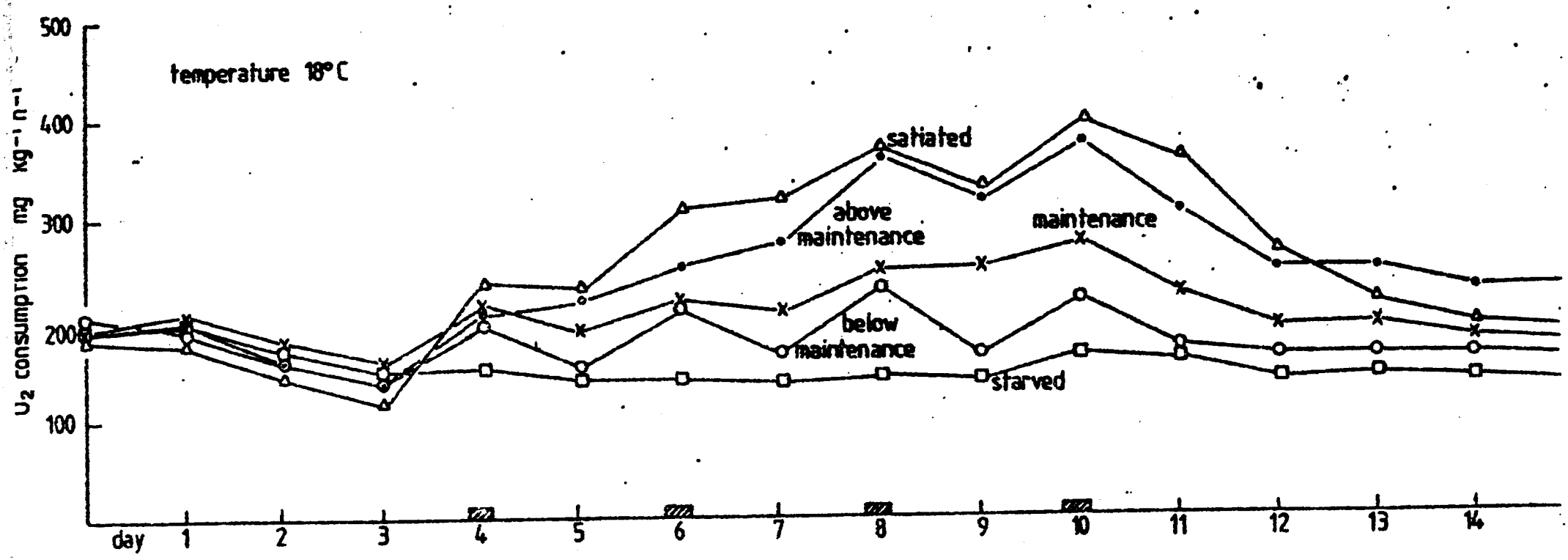

Figure 6 Oxygen consumption of fish with time where each point is a mean reading taken over 24 hours. Days on which the fish were fed are hatched.

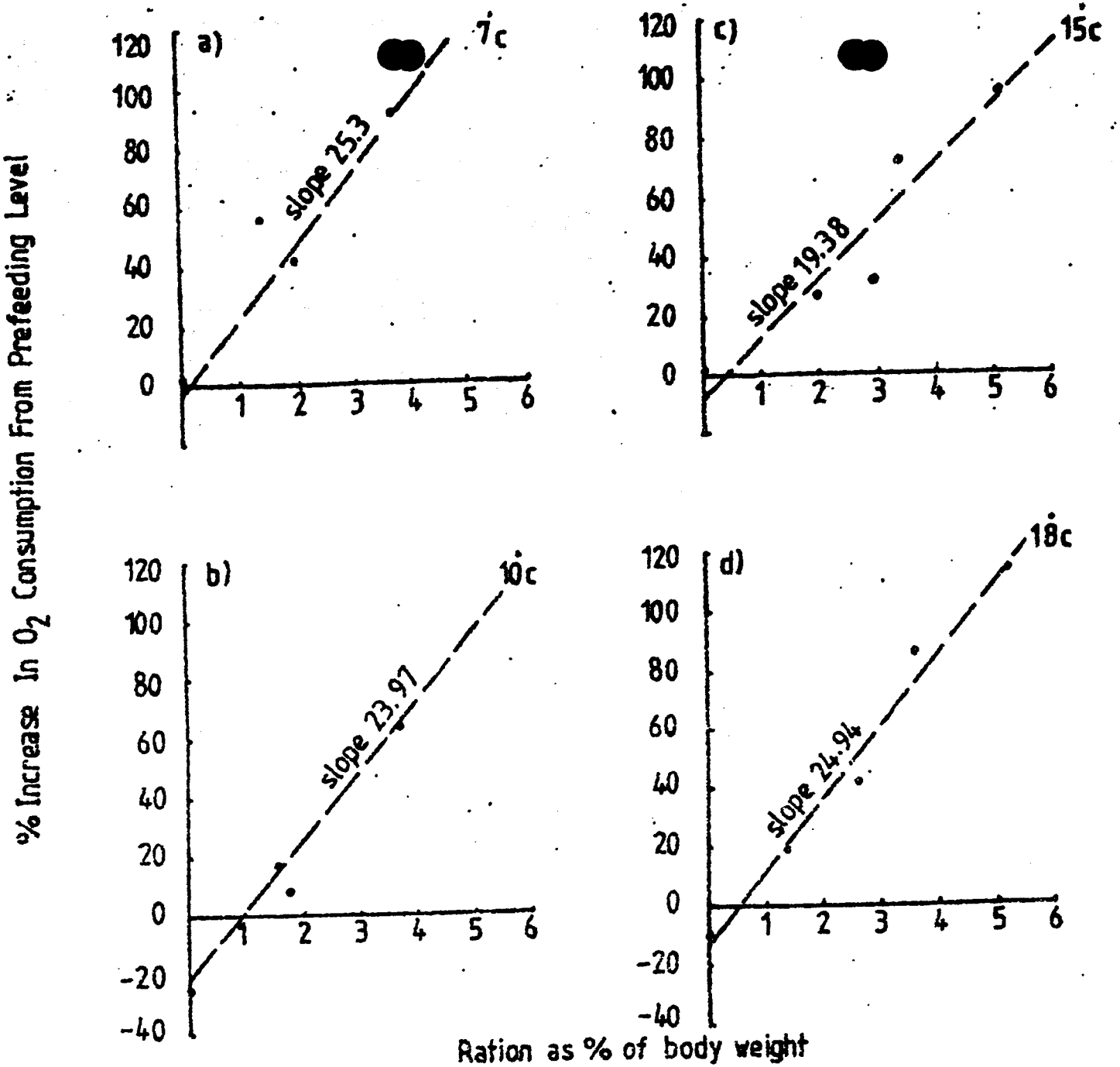

Figure 7 Relationship between ration and % increase in O_2 consumption from pre-feeding level at different temperature. Each print is a mean reading taken over feeding period

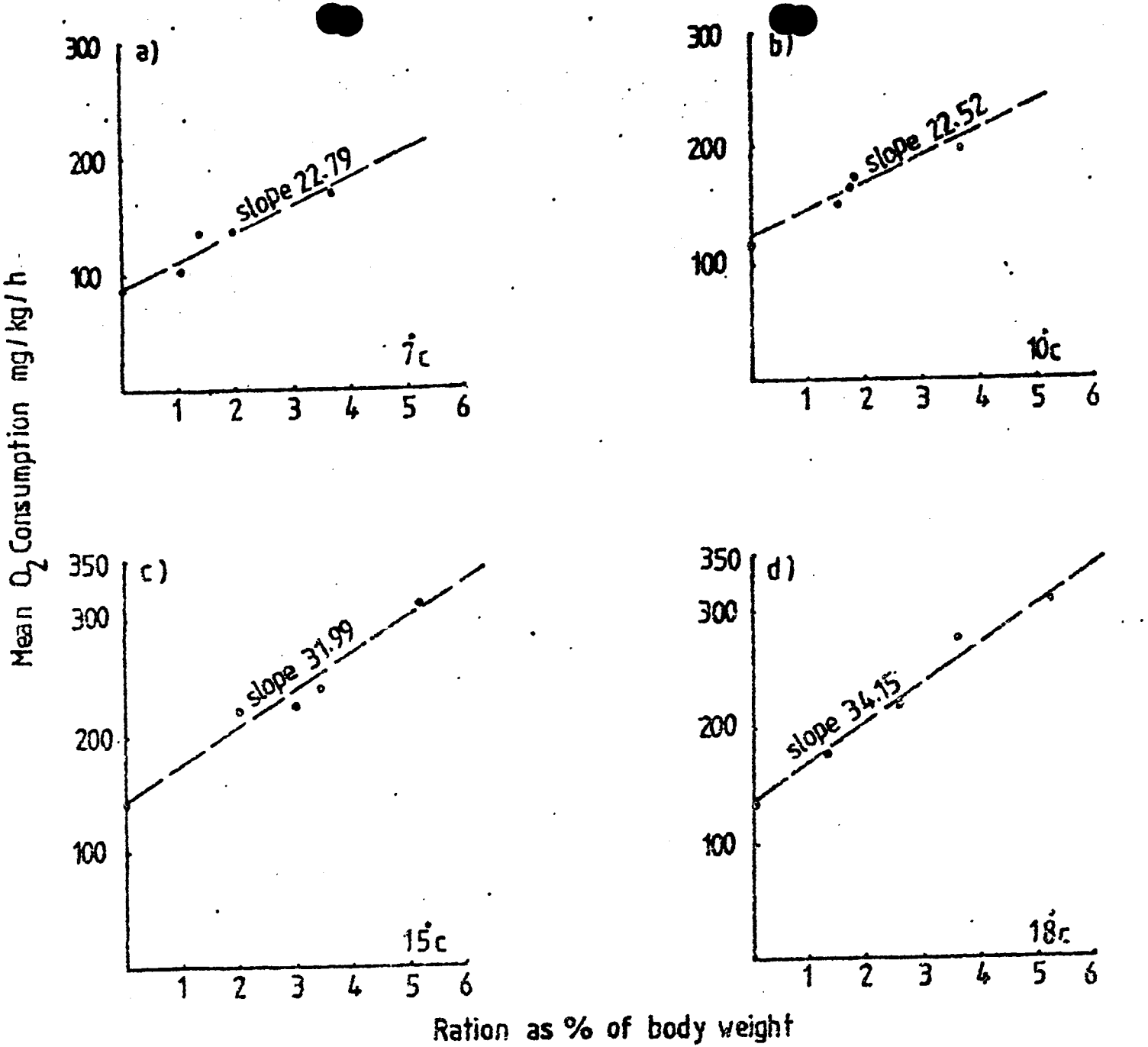

Figure 8 Relationship between ration size and mean oxygen consumption at different temperature. Each point is a mean reading taken over feeding period.

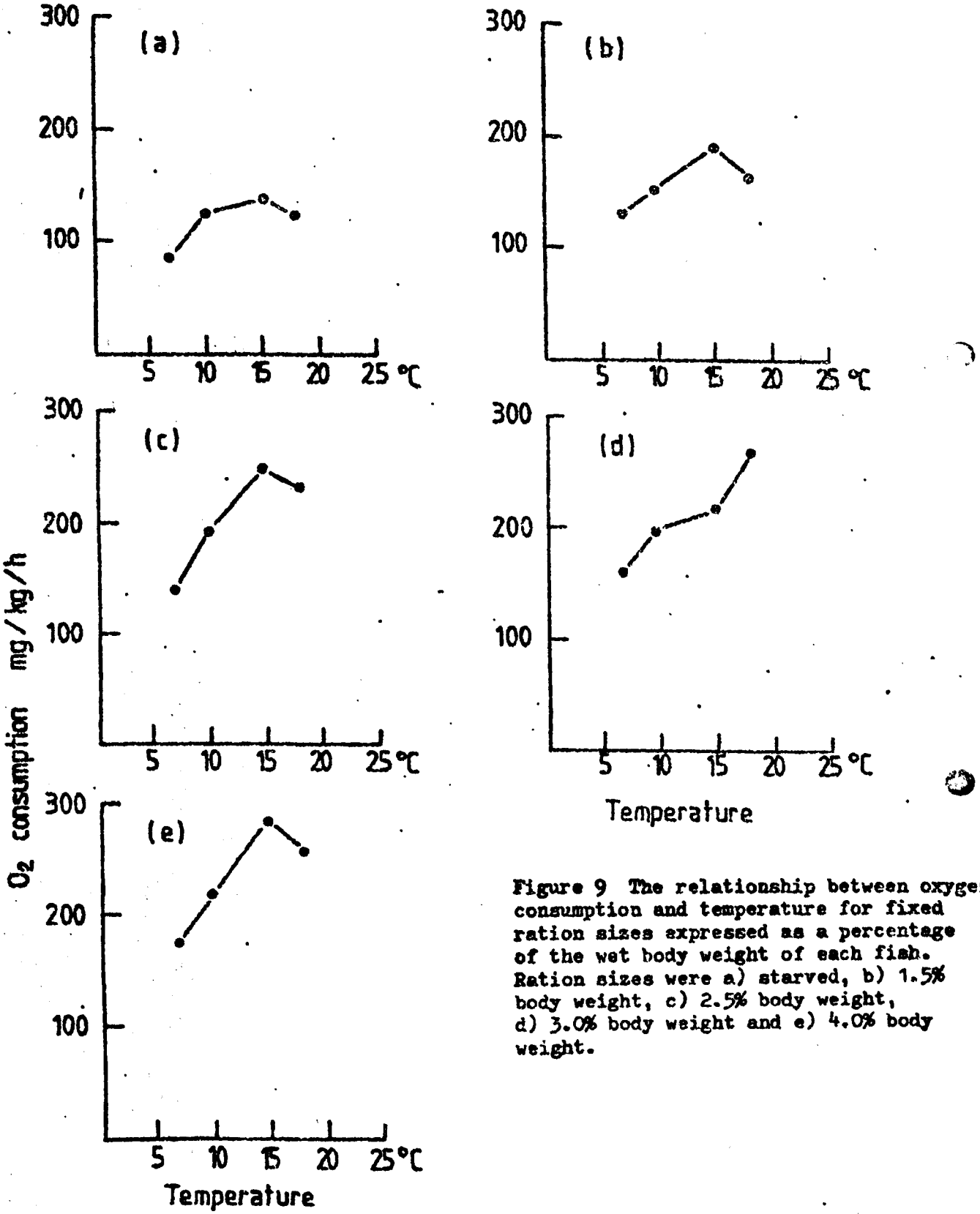

Figure 9 The relationship between oxygen consumption and temperature for fixed ration sizes expressed as a percentage of the wet body weight of each fish. Ration sizes were a) starved, b) 1.5% body weight, c) 2.5% body weight, d) 3.0% body weight and e) 4.0% body weight.