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GILL AND BODY SURFACE AREAS OF THE CARP IN RELATION TO BODY MASS, WITH SPECIAL REFERENCE TO THE METABOLISM-SIZE RELATIONSHIP

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SUMMARY

The relationships of resting metabolism per unit mass of body to gill and body surface areas were examined by measuring gill, body surface and fin areas of carp ranging from 0·0016 to 2250 g. There was a triphasic allometry for the relationship between gill area and body mass: during the prelarval (0·0016–0·003 g) and postlarval (0·003–0·2 g) stages there was a positive allometry (slopes of 7·066 and 1·222, respectively), during the juvenile and later stages (0·2–2250 g) there was a negative allometry with a slope of 0·794. There was a diphasic negative allometry for the relationship between surface area of the body or the fins and body mass, with a slope of 0·596 or 0·523 during the larval stage and 0·664 or 0·724 during the juvenile and later stages, respectively. Except for the 3rd phase (juvenile to adult) of gill area, these slopes were significantly different ($P < 0·01$) from the slope for the relationship between resting metabolism and body mass of intact carp (0·84; value from Winberg, 1956). It is considered, therefore, that gill, body surface and fin areas do not directly regulate the resting metabolism of the fish, in the larval stage at least.

INTRODUCTION

The mass-specific rate of basal metabolism decreases with increasing body mass. This phenomenon has been widely observed and repeatedly discussed in various animals including fishes (Winberg, 1956; Hemmingsen, 1960; Kleiber, 1961; Paloheimo & Dickie, 1966; Schmidt-Nielsen, 1970; Brett & Groves, 1979; Heusner, 1982; Feldman & McMahon, 1983; Hughes, 1984*a*; Wieser, 1984; and many others). The relationship between basal metabolic rate of animals (M) and the body mass (W) is expressed, both intraspecifically and interspecifically, by the allometric equation, $M = aW^b$, where a and b are constants. Because the mass exponent b is smaller than unity, the mass-specific metabolic rate (M/W) decreases with increasing body mass.

This phenomenon was formerly explained by the so-called 'surface rule' in terms of homoiothermy (Rubner, 1883). However, a similar relationship was also shown for poikilotherms. The mass exponent b was later found to be not 2/3, which is the mass

Key words: Gill area, body surface area, fin area, metabolism-size relationship, carp.

exponent of the body surface, but 3/4 in mammals and birds (Kleiber, 1932) and about 0·85 in fishes (Ricker, 1973, calculated from the data of Winberg, 1956; Brett & Groves, 1979).

It was later suggested that the phenomenon was the result of a decrease in mass-specific rate of tissue respiration (Q_{O_2}) with increasing body mass; however, the slopes of the relationships between Q_{O_2} and body mass in most tissues are not large enough to explain the phenomenon in intact animals (Krebs, 1950; Von Bertalanffy & Pirozynski, 1953; Girard & Grima, 1980; Oikawa & Itazawa, 1984*a*).

On the other hand, the slopes for the respiratory area-body mass relationship have been argued to be similar to the slopes for the metabolism-body mass relationship (Ludwig, 1956; Balke, 1957; Von Bertalanffy, 1957; Whitford & Hutchison, 1967; Ultsch, 1973, 1976). In fishes, morphometric studies on the relationship between gill area and body mass have been carried out in many species (Price, 1931; Byczkowska-Smyk, 1961; Ursin, 1967; Muir, 1969; Muir & Hughes, 1969; Suzuki, 1969; Hughes, 1970, 1978; Hughes, Dube & Munshi, 1973; Hughes *et al.* 1974; De Silva, 1974; Holeton, 1976; Hakim, Munshi & Hughes, 1978), and there have been excellent morphological studies on the development of the gill system (Byczkowska-Smyk, 1961; Morgan, 1974*a,b*). Most of these studies, however, were devoted to limited stages in the life history of the fish, although Price (1931) examined the dimensions of the gill sieve in small-mouthed black bass of 0·33–840 g. There have been few measurements of the area of the body surface that is considered to play an important role in gas exchange during early development.

We here present the results of morphometric studies on the allometric relationships of gill, body surface and fin areas to body mass of carp ranging from 2-day-old larvae of 0·0016 g to the adults of 2250 g, and we discuss the relationship between surface area and metabolism.

MATERIALS AND METHODS

Measurements of gill, body surface and fin areas were carried out on 32 carp, *Cyprinus carpio*, ranging from 0·0016 g (2 days after hatching and at the stage at which the gill secondary lamellae became clearly recognisable) to 2250 g. The fish smaller than 30 g were raised at 20 °C in our laboratory and were fed on live water fleas, *Daphnia pulex*, for a week beginning 2 days after hatching and then on marketed carp diet made from fish meal, wheat flour, soybean cake, vitamins and minerals as well as water fleas. The fish larger than 30 g were raised at a commercial fish farm and transported to our laboratory.

The fish of under 100 g were fixed whole in formalin Cortland saline made from one part of concentrated formalin and nine parts of Cortland saline (Wolf, 1963). With the fish of over 100 g, the gills together with the gill arches were excised and fixed in the formalin Cortland saline. The results of measurements with the fixed materials were converted to the figures with the fresh ones based on the average shrinking coefficients estimated from carp of 0·054–200 g; i.e. 2·9 % for filament length, 4·3 % for body length, 5·7 % for gill area, 7·3 % for body surface and fin areas, and − 2·4 % (2·4 % increase) for body mass.

The gill area or the total bilateral area of the secondary lamellae (A) was estimated,

after Hughes (1966, 1984*b*), by the formula

$$A\ (\mathrm{mm}^2) = (2L/d')bl,$$

where L is the total length of all the filaments (mm), $1/d'$ is the average spacing of the secondary lamellae on one side of the filaments (mm^{-1}) and bl is the average bilateral area of the secondary lamellae (mm^2). It should be noted that bl is not $b \times l$ both of which are described later.

The total length of all the filaments (L) was determined by doubling the estimate of the filament length of all the gill arches on the left side of the body, obtained by measuring the length of every filament from small fish of 0·0016–1·3 g and every third or fifth filament from fish of 2·2–2250 g.

The spacing of the secondary lamellae on one side of the filaments was determined from measurements of all the lamellae on the filaments of average length in the dorsal, middle and ventral parts of all the gill arches on the left side of the body in small fish of 0·0016–0·33 g. In fish of 1·3–2250 g, the second left arch was examined. The average spacing was estimated by the weighted mean method, which takes into account the difference in length of different filaments, although the spacing was not very different among different filaments and among different regions on a filament.

The area of the secondary lamellae was determined with the lamellae chosen at almost regular intervals on the filaments of average length in the dorsal, middle and ventral parts of the second gill arch on the left side of the body, except for very small fish of 0·0016–0·014 g in which all the left gill arches were used. The number of lamellae chosen for the measurement ranged from 9 in the fish of 0·0016 g to 236 in the fish of 2250 g, with exceptional cases in which 380 and 1475 lamellae were chosen from the fish of 532 g and 660 g, respectively. Twice the value of a lamellar area was regarded as the area of the lamella, considering both sides of the lamella to function as the site for gas exchange. The average value of the bilateral lamellar area was estimated by the weighted mean method, which takes account of the lengths of different filaments, because the area and shape of the lamellae varied considerably among different filaments and among different regions on a filament.

The area of a lamella was determined by both or either one of the following two methods, depending on fish size. In the triangle method, as used by Price (1931) but not Hughes (1966, 1984*b*), applied to small fish of 0·0016–6·5 g, the area of a lamella was calculated, assuming it to be a triangle, from the maximum height (b) and the base length (l) of the lamella measured from a magnified figure traced on paper by means of a microscope and a *camera lucida*. In very small fish of 0·0016–0·014 g, it was difficult to measure the base length, and so this was estimated from the maximum height and body mass (W) using the formula, obtained with nine fish of 0·0028–1·3 g, $l/b = 2{\cdot}01W^{0{\cdot}130}$ [the correlation coefficient between log (l/b) and log W was 0·897]. In fish of 2·2–2250 g, the area of a lamella was directly measured using a section of 90–150 μm cut by the freezing method from a filament embedded in gelatine and stained with diluted Giemsa solution. The lamellar area was obtained by tracing, with a planimeter, the outline of a magnified figure of the sectioned lamella. The apparent value of the lamellar area obtained by this method was converted to the real value, allowing both for angular bias of the section from the lamellar axis and for shrinkage of the lamella by fixing.

The area of the magnified figure of a sectioned lamella was measured by both the triangle and the direct methods, and the results were compared. The relationship of the value of the lamellar area determined by the direct method (bl) to the value estimated by the triangle method (bl') in seven fish of 2·2–2250 g was expressed by the formula, $bl/bl' = 1{\cdot}48W^{-0{\cdot}026}$ [the correlation coefficient between log (bl/bl') and log W was $-0{\cdot}805$]. The value of the lamellar area obtained by the triangle method was, therefore, converted to the real value based on this formula.

The basal part of the secondary lamella is embedded in the tissue bed of the gill filaments, and the part responsible for gas exchange is considered to be the exposed part of the lamella. The values of the lamellar area obtained by the triangle method in small fish of 0·0016–6·5 g were considered to be the values of the whole lamellae including the embedded part, although the boundary line between the exposed part and the embedded one was not clear, because the line showing the relationship between the lamellar area obtained by the triangle method and body mass was approximately on the extension of the line for the whole lamellar area-body mass relationship in bigger fish of 2·2–2250 g (Fig. 1). The values of the lamellar area obtained in the small fish were therefore converted to the values for the exposed part using the formula for the ratio of the exposed part to the whole lamella (R), $R = 0{\cdot}76W^{-0{\cdot}037}$, obtained with seven fish of 2·2–2250 g (the correlation coefficient between log$R$ and log$W$ was $-0{\cdot}680$).

Body surface area was obtained, in large fish above 100 g, by multiplying the body length by the average circumference of the body measured at ten evenly-spaced transverse sections of the body. In small fish under 100 g, the body surface area was estimated from body heights and body widths of the ten evenly-spaced parts using the following parabolic equation, assuming the circumference to be

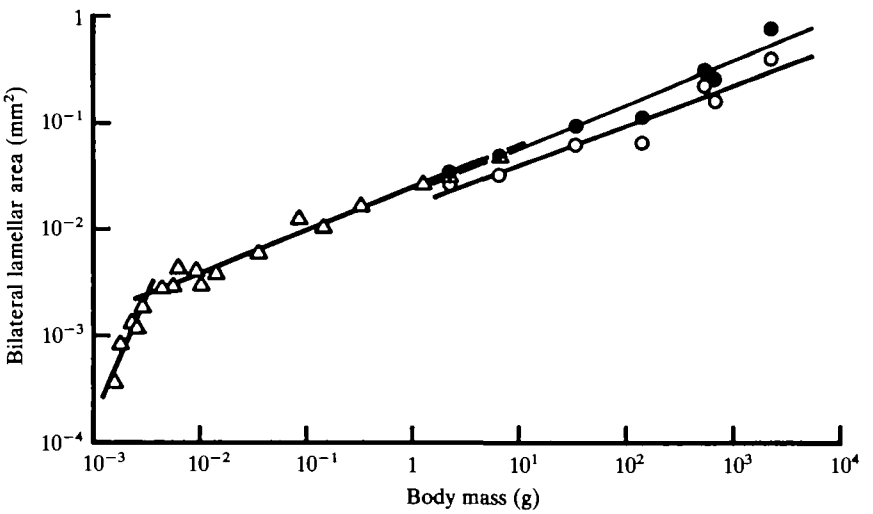

Fig. 1 Comparison between average bilateral areas of the gill secondary lamellae determined by two methods, the triangle method (△) and the direct method (● : whole area including the embedded part; ○ : area of the exposed part).

composed of two parabolas,

$$C = \sqrt{4H^2 + B^2} + \frac{B^2}{2H} \times \ln \frac{2H + \sqrt{4H^2 + B^2}}{B},$$

where C is circumferential length, H is body height, and B is body width. The body surface area estimated by this equation was found to be 8·3 % smaller than the directly measured area in fish of 140–2250 g. Therefore, the estimated values were multiplied by 1·09 to convert them to the real values. Fin area was directly measured by tracing, with a planimeter, the outline of the magnified figure of the fin fixed in formalin Cortland saline.

RESULTS

There was a triphasic allometry between gill area and body mass of the carp: the allometry was positive in the 1st and the 2nd phases and negative in the 3rd phase (Fig. 2). The fish developed from the 1st to the 2nd phase, when the larvae were about 7 days old, weighed about 0·003 g and when the yolk had been almost absorbed. They developed from the 2nd to the 3rd phase, when they were about 40 days old, weighed about 0·2 g, and when the fins had assumed the adult form and the scales had begun to appear. Therefore, we consider that the 1st phase corresponds to the prelarval

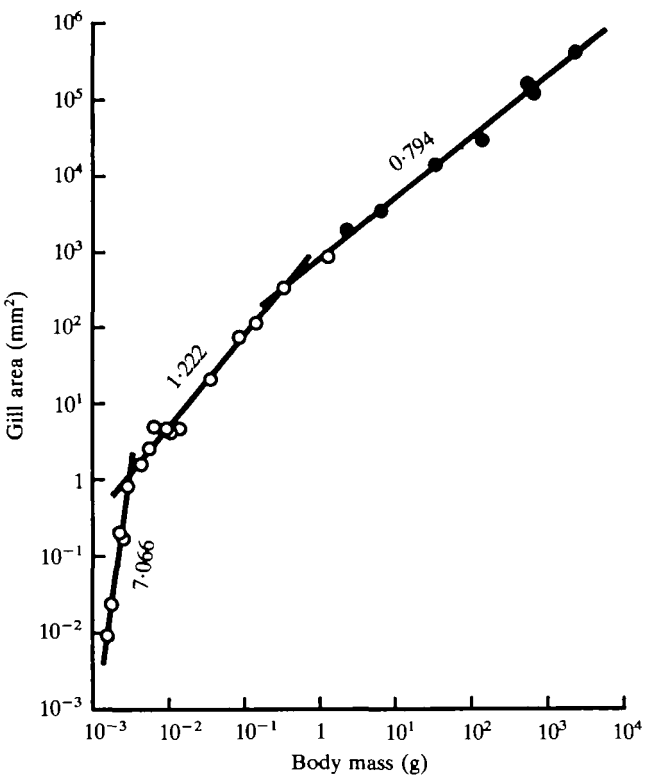

Fig. 2 Allometric relationships of the gill area to body mass. Open circles show the values estimated by the triangle method, and solid circles the values by the direct method. Figures by the regression lines indicate the slopes of the lines.

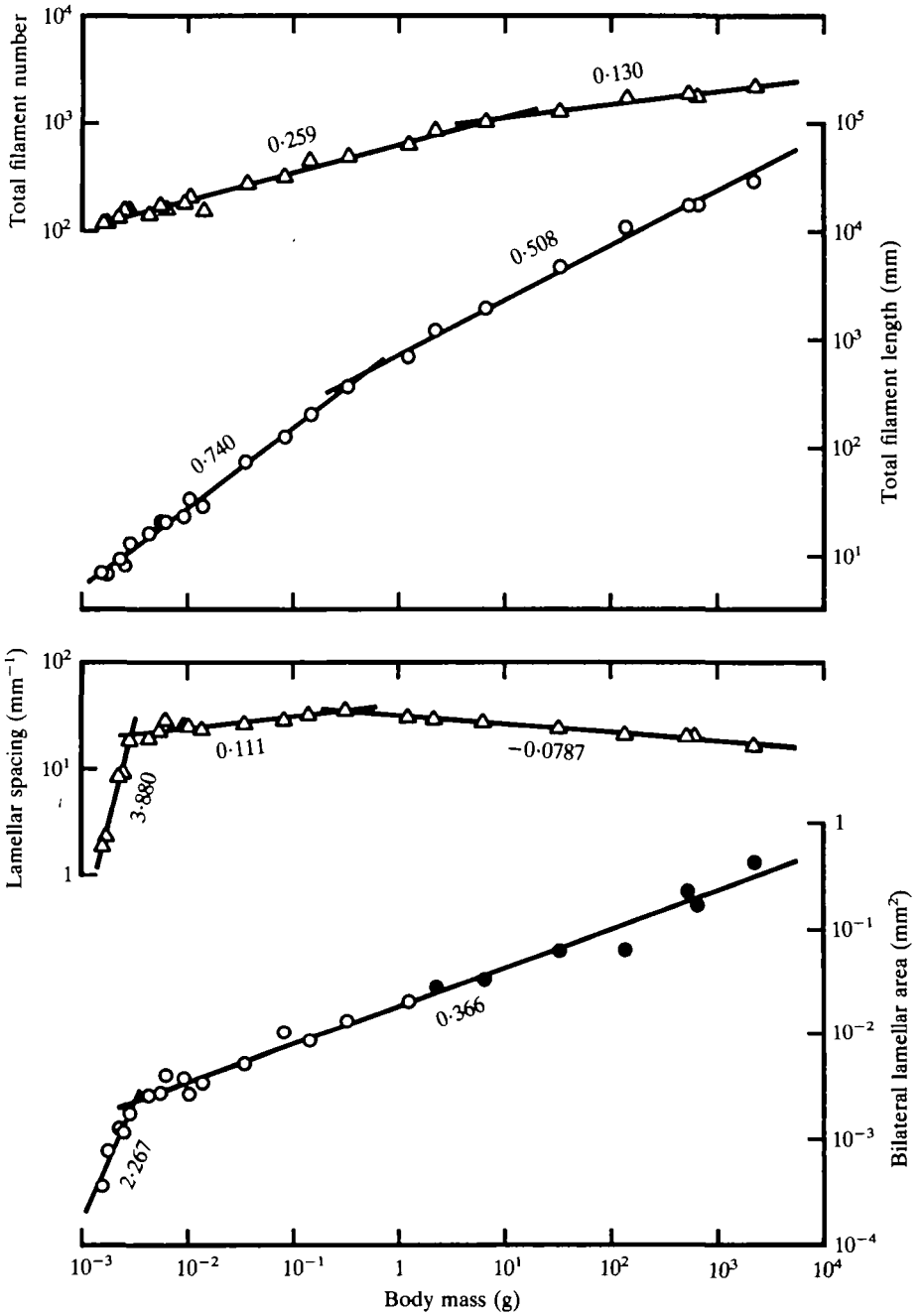

Fig. 3 Allometric relationships of the total filament number, the total filament length, the average spacing of the gill secondary lamellae on one side of the filament, and the average bilateral area of the lamellae, to body mass. Symbols for the lamellar area are the same as those in Fig. 2. Figures by the regression lines indicate the slopes of the lines.

Table 1. *Regression analyses of the allometric relationships* ($Y=\alpha W^{\beta}$) *of the gill dimensions* (Y) *to body mass* (W)

Y	Range of body mass (g)	*N*	α	β ($\bar{X} \pm$ S.E.)	*r*
Gill area (mm^2)	0·0016–0·0028	5	$6{\cdot}74 \times 10^{17}$	7·066 ±0·934	0·975
	0·0028–0·33	11	1334	1·222 ±0·055	0·991
	0·33–2250	9	846	0·794 ±0·025	0.997
Total filament number	0·0016–6·5	18	635	0·259 ±0·0099	0·988
	6·5–2250	6	823	0·130 ±0·016	0·970
Total filament length (*L*, mm)	0·0016–0·33	15	835	0·740 ±0·021	0·995
	0·33–2250	9	719	0·508 ±0·017	0·996
Spacing of the secondary lamellae ($1/d'$, mm^{-1})	0·0016–0·0028	5	$1{\cdot}32 \times 10^{11}$	3·880 ±0·417	0·983
	0·0028–0·33	11	40·3	0·111 ±0·023	0·846
	0·33–2250	9	32·2	−0·0787 ±0·0039	−0·991
Average bilateral area of the secondary lamellae (*bl*, mm^2)	0·0016–0·0028	5	1053	2·267 ±0·515	0·931
	0·0028–2250	19	$1{\cdot}85 \times 10^{-2}$	0·366 ±0·012	0·991

stage, the 2nd phase to the postlarval stage, and the 3rd phase to the juvenile and later stages.

These transitions in the allometric relationships of gill area to body mass were closely correlated with changes following body mass increase in the total filament

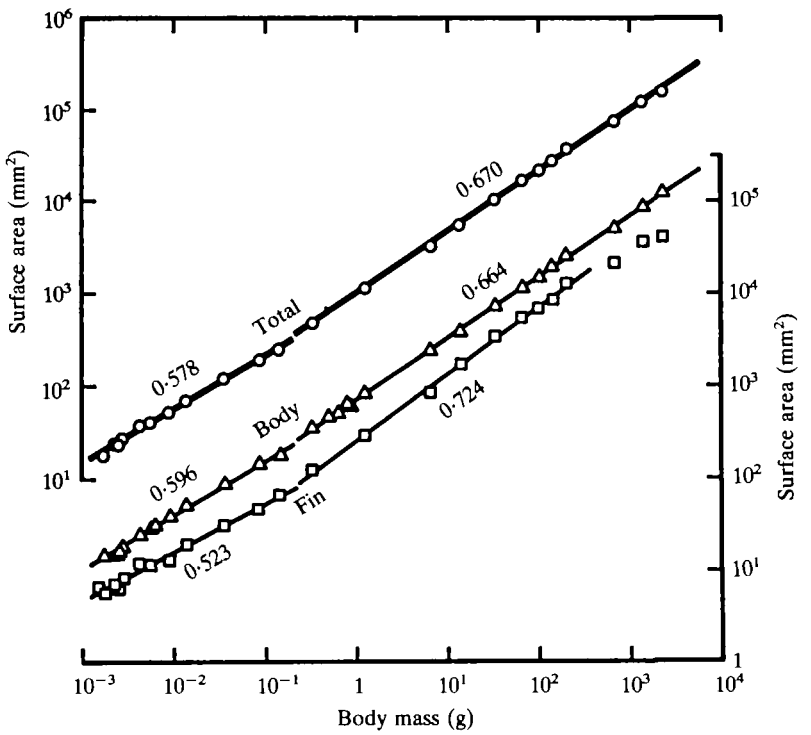

Fig. 4 Allometric relationships of body surface area (△), bilateral fin area (□) and the total surface area (○) to body mass. The total surface area means the sum of the body surface area and the bilateral fin area. Figures by the regression lines indicate the slopes of the lines.

Table 2. *Regression analyses of the allometric relationships* ($Y = \alpha W^{\beta}$) *of body surface, fin areas or total surface areas* (Y) *to body mass* (W)

Y	Range of body mass (g)	N	α	β ($\bar{X} \pm$ S.E.)	r
Body surface area (mm^2)	0·0018–0·14	12	616	0·596 ± 0·0077	0·999
	0·33–2250	16	719	0·664 ± 0·0032	0·9998
Bilateral fin area (mm^2)	0·0016–0·14	12	176	0·523 ± 0·0194	0·993
	0·33–200	9	255	0·724 ± 0·0133	0·999
Total surface area (mm^2)	0·0018–0·14	11	794	0·578 ± 0·0086	0·999
	0·33–2250	12	989	0·670 ± 0·0059	0·9996

length, the average spacing of the secondary lamellae on one side of the filaments, and the average area of the secondary lamellae (Fig. 3; Table 1).

Surface area of both body and fins showed diphasic negative allometry corresponding to the larval stage and the juvenile and later stages (Fig. 4; Table 2). Slopes for both body surface and fin areas in the larval stage were significantly smaller than 2/3 ($P < 0{\cdot}001$), while the slopes in the juvenile and later stages were nearly 2/3 for body surface area and larger than 2/3 for fin area ($P < 0{\cdot}01$).

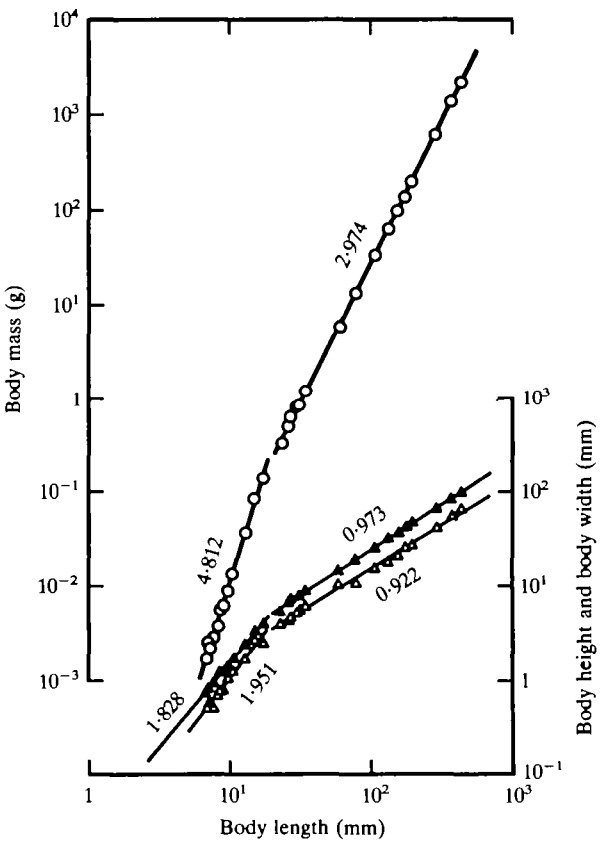

Fig. 5. Allometric relationships of body mass (○), the mean body height (▲) and the mean body width (△) to body length. Figures by the regression lines indicate the slopes of the lines.

Table 3. *Regression analyses of the allometric relationships* ($Y=\alpha L^{\beta}$) *of body mass, mean body height and mean body width* (Y) *to body length* (L)

Y	Range of body length (mm)	*N*	α	β ($\bar{X} \pm$ S.E.)	*r*
Body mass (g)	6·93–17·2	12	$1{\cdot}70 \times 10^{-7}$	$4{\cdot}812 \pm 0{\cdot}100$	0·998
	23·0–430	16	$3{\cdot}18 \times 10^{-5}$	$2{\cdot}974 \pm 0{\cdot}016$	0·9998
Mean body height (mm)	6·93–17·2	12	$2{\cdot}24 \times 10^{-2}$	$1{\cdot}828 \pm 0{\cdot}053$	0·996
	23·0–430	16	$2{\cdot}69 \times 10^{-1}$	$0{\cdot}973 \pm 0{\cdot}0093$	0·999
Mean body width (mm)	6·93–17·2	12	$1{\cdot}16 \times 10^{-2}$	$1{\cdot}951 \pm 0{\cdot}122$	0·981
	23·0–430	16	$2{\cdot}15 \times 10^{-1}$	$0{\cdot}922 \pm 0{\cdot}021$	0·996

The transition in the allometric relationships of body surface area to body mass was accompanied by a change in body form (Fig. 5). The results of regression analyses of the allometric relationships showing the body form are shown in Table 3. Body mass, mean body height and mean body width showed diphasic allometry, with an inflexion point at about 18 mm for body length and about 0·2 g for body mass. The slope in the 2nd phase was almost 3 for body mass and almost 1 for body height and body width, while the slopes in the 1st phase were much larger ($P < 0{\cdot}001$).

DISCUSSION

The morphometric results (Fig. 5; Table 3) indicate that the body form of the carp changes remarkably in the larval stage, but then changes little in the juvenile and later stages. The morphometry of the gills also showed the most remarkable changes in the early stages (Figs 2, 3). These observations are consistent with those of De Silva (1974), on herring and plaice, that the slope for the relationship of gill area to body mass and the slopes for the relationships of the total filament length, the lamellar spacing on the filaments, and the average area of the secondary lamellae to body mass are steeper before metamorphosis than after it. The observations are also consistent with those of McDonald & McMahon (1977), on Arctic char, that the gill area, the total number and the average area of the secondary lamellae, and the total filament number rapidly increase during the stages of 2–47 days old (0·067–0·099 g). The relationship of the total filament number to body mass is described as diphasic allometry in the present paper, but the rate of increase in filament number in the 2nd phase seems not to be constant but to diminish gradually, as described by Price (1931) in the small-mouthed black bass.

The gill area of the carp showed diphasic positive allometry with slopes of 7·066 and 1·222 during the larval stage (0·0016–0·33 g) and monophasic negative allometry with a slope of 0·794 during the juvenile and later stages (0·33–2250 g). Price (1931) described monophasic negative allometry with a slope of 0·785 in the gill area of small-mouthed black bass of 0·33–840 g. The slopes in fish larger than 0·33 g are almost the same in both species. The positive allometry with steep slopes during the larval stage of the carp means that the gill area per unit body mass is very small in the early larval stage and rapidly increases during the larval stage. The gill area per unit body mass calculated on the basis of the allometric equations (Table 1) is 7·4 $mm^2 g^{-1}$ at a body

mass of 0·0016 g, and increases to 370 $mm^2 g^{-1}$ at 0·003 g and 1100 $mm^2 g^{-1}$ at 0·35 g, and then decreases to 180 $mm^2 g^{-1}$ at 2000 g. The areas per unit body mass of the total surface (body surface and fin surface) are calculated from data in Table 2 to be 12 000, 9200, 1400 and 81 $mm^2 g^{-1}$ at the corresponding body masses of 0·0016, 0·003, 0·35 and 2000 g, respectively. We therefore consider that cutaneous respiration through the body and fin surfaces plays an important role during the early stages in the life history of fish. During the larval stage in the carp, the duct of Cuvier on the enlarged anterior part of the yolk and dense nets of vessels in the dorsal finfold have been considered to be important sites of gas exchange (Balon, 1975). In the prelarval stage, the yolk gradually diminishes in size as it is absorbed by the larva. At the same time, the gill area rapidly increases compensating for the loss of respiratory vessels in the yolk. In the postlarval stage, the relative importance of cutaneous respiration continues to decrease gradually, but at a slower rate than in the prelarval stage. In contrast, the relative importance of gill respiration increases with growth. For the body surface and fin areas, the slopes in the larval stage were smaller than 2/3. This means that smaller fish have larger mass-specific areas of body surface and fins which compensate for the smaller gill area in the earlier stage. The absence of scales during the larval stage probably facilitates gas exchange through the body surface. These features are consistent with the often emphasised phenomenon that the cutaneous gas exchange is relatively more important during the earlier stages in the life history of fish than in the later stages (Fry, 1957; Blaxter, 1969; De Silva, 1974; Balon, 1975; Iwai & Hughes, 1977; McDonald & McMahon, 1977; McElman & Balon, 1980).

Comparison of the results of morphometric study on carp gills by the present authors with those by Saunders (1962) and Hughes & Morgan (1973) is given, for fish of the same size, in Table 4. Although the values for lamellar spacing are not very different, the filament number is smaller, and both the lamellar number and the gill area are larger in the present study than in that of Saunders (1962) or Hughes & Morgan (1973), for fish of 184 g, 531 g or 878 g. The differences in the filament and lamellar numbers are probably caused by the different populations and the different rearing conditions, since they are gill dimensions that can be measured relatively accurately. The difference in the gill area is probably caused by the different populations and/or different technical procedures. If the gill areas of fish of 184 g, 531 g and 878 g in the present study are calculated ignoring the shrinkage coefficient (5·7 %) and the error in the triangle method (23 % for fish of 184 g, 20 % for one of 531 g and 19 % for one of 878 g estimated by the equation $bl/bl' = 1{\cdot}48W^{-0{\cdot}026}$), the values of the gill area become 210, 175 and 160 $mm^2 g^{-1}$, respectively, which are closer to the values obtained by Saunders (1962) and Hughes & Morgan (1973) than to our values in the present study.

In many species of fish, resting metabolism has been considered to be proportional to about the 0·85 power of body mass (Ricker, 1973; Brett & Groves, 1979). In carp, the exponent has been reported to be 0·84 in fish of 0·0032–3500 g (Winberg, 1956). We obtained a very similar figure, 0·832, in carp of 0·0019–620 g (Y. Itazawa & S. Oikawa, in preparation). On the other hand, the present study showed that the gill area was proportional to the 7·066, 1·222 or 0·794 power of body mass depending on the developmental stages, while the total surface area was proportional to the 0·578 or 0·670 power of body mass. The slopes for the surface areas are significantly

Table 4. *Comparison of the gill dimensions of carp in the present study and in previous reports*

Body mass (g)	Total no. of filaments	Secondary lamellae mm^{-1} filament of one side	Total no. of secondary lamellae	Average area of secondary lamellae (mm^2)	Gill area ($mm^2 g^{-1}$)	Reference
19	–	20·8	168 000	0·060†	526	Saunders (1962)
	1207	25·5	164 000	0·054	461	Present study
184	–	20·7	348 000	0·076†	145	Saunders (1962)
	1621	21·4	434 000	0·125	289	Present study
531	2567	20·0	491 000*	0·150†	139	Hughes & Morgan (1973)
	1861	19·7	685 000	0·184	232	Present study
878	–	17·9	634 000	0·189†	137	Saunders (1962)
	1986	18·9	850 000	0·221	209	Present study

* Arithmetic mean of 348 000 and 634 000, figures in Saunders (1962).
† Calculated by substituting figures in the original papers for the terms of the formula, gill area ($mm^2 g^{-1}$) × body mass (g)/total number of secondary lamellae.

different from the slope for metabolism-body mass relationship ($P < 0{\cdot}01$), except for the 3rd phase of gill area. We consider, therefore, that neither gill nor body surface areas directly regulate the resting rate of metabolism of the fish, in the larval stage at least.

The similarity of the slope for the gill area-body mass relationship during the juvenile and later stages to the slope for the resting metabolism-body mass relationship suggests that the mass-specific metabolic rate in these stages may be dependent on gill area. However, if other factors constrain the slope for the metabolic rate, in relation to body mass, to be approximately 0·85 throughout the whole range of body mass, this will give a better interpretation of the decline in mass-specific metabolic rate of the animal. We have previously (Itazawa & Oikawa, 1983) proposed that 'the decline in weight-specific rate of basal metabolism of an intact animal with increasing body size could be explained, partly at least, if tissues with low metabolic rates (Q_{O_2}) get larger with growth in weight in proportion to the whole body'. This hypothesis is now being examined, based on the Q_{O_2} values of various tissues (Oikawa & Itazawa, 1984*a*) and the relative growth of the tissues (Oikawa & Itazawa, 1984*b*) using carp of a wide range in body mass.

The gill area is considered to be concerned with the active metabolism rather than the resting metabolism. It has been reported in various animals that the slope for the active metabolism-body mass relationship is steeper than that for the resting metabolism-body mass relationship, and therefore larger animals have larger scope for activity (Brett, 1965, 1972; Hughes, Gaymer, Moore & Woakes, 1971; Brett & Glass, 1973; Hughes, 1984*a*). In sockeye salmon, the active metabolism has been reported to be proportional to the 0·97 power of body mass, while the resting metabolism is proportional to the 0·78 power of body mass (Brett, 1965). Hughes (1977) indicated that the slope for gill area-body mass relationship was larger than the slope for resting metabolism-body mass relationship, especially in salmon and trout.

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