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THE INFLUENCE OF BLOOD GAS PROPERTIES ON GAS TENSIONS AND pH OF VENTRAL AND DORSAL AORTIC BLOOD IN FREE-SWIMMING TUNA, *EUTHYNNUS AFFINIS*

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SUMMARY

We have developed a technique for capture, anaesthetization, instrumentation and release of tuna and have made the first determinations of blood gas values in dorsal and ventral aortae of free-swimming tuna. Dorsal aortic P_{O_2} varied from 34·5 to 91·7 mmHg, and P_{CO_2} ranged from 3·7 to 7 mmHg. Dorsal aortic blood [pHa = 7·77 ± 0·04 (8), mean ± one S.E.M. (*N*)] was more alkaline than ventral aortic blood [pHv = 7·65 ± 0·02 (7)]. Warming dorsal aortic blood from 25 to 35 °C in a closed system caused P_{O_2} and P_{CO_2} to rise and pH to fall. Oxygen-combining curves for whole blood were sigmoid [mean Hill's number = 1·72 ± 0·05 (11), range 1·57–2·0] and P_{50} over the pH range found in free-swimming animals was 21 ± 1·75 (8) mmHg. The CO_2-induced Bohr coefficient ($\Delta \log P_{50}/\Delta$ pH) was −0·59 ± 0·046 (30). Unusual features of CO_2-combining curves are attributed to a significant Root effect. Although these *in vitro* properties of tuna whole blood are at variance with other published data on tuna they nevertheless substantiate our determinations made *in vivo*.

INTRODUCTION

In a recent paper, Cech, Laurs & Graham (1984) reported some unusual features of the oxygen-combining properties of whole blood of freshly caught albacore tuna (*Thunnus alalunga*). They found that the oxygen dissociation curve was hyperbolic (Hill's number = 1·1) with an extremely low P_{50} (about 8 mmHg) even at 25 °C. There was a strong Bohr effect (Bohr coefficient = −1·17), a negligible Root effect, and a reverse temperature effect with $\Delta H = +1{\cdot}72$ kcal mol^{-1} (at 0 % CO_2) and $\Delta H = +0{\cdot}26$ kcal mol^{-1} (at 1 % CO_2). Unusual temperature effects on tuna haemoglobin solutions and whole blood have been reported previously (Rossi-Fanelli & Antonini, 1960; Sharp, 1975; Carey & Gibson, 1977, 1983; Ikeda-Saito, Yonetani & Gibson, 1983) and have provided a basis for models describing how oxygen transfer from the arterial to venous circulation would be minimized when blood is warmed in

Key words: oxygen dissociation, Bohr coefficient, Root effect.

the vascular heat exchanger before going to the muscles (Carey & Gibson, 1983; Cech *et al.* 1984).

Using these observations on whole blood, together with parameters chosen to illustrate performance of models, we can predict what the consequences would be for tuna going about their daily business. High ventilation volumes (Stevens, 1972) and large gill areas of tuna (Muir, 1969; Muir & Hughes, 1969) support claims that arterial P_{O_2} will be high and P_{CO_2} low. In fact, low P_{CO_2} is a prerequisite for effective performance of the models because the reverse temperature effect is greatly reduced by increasing CO_2 in the blood (Cech *et al.* 1984). The low P_{50} obtained by Cech *et al.* (1984) suggests that ventral aortic P_{O_2} will be low (< 8 mmHg) if the animal is going to extract enough oxygen from arterial blood. Finally, the linkage equation states that the Bohr coefficient is identical to the Haldane coefficient (Wyman, 1964; Heck, 1970); if this holds for whole blood, as well as haemoglobin solutions, then if the Bohr coefficient exceeds $-1{\cdot}0$ dorsal aortic blood will be less alkaline than ventral aortic blood unless the RQ is also greater than 1·0.

Obviously, it is possible to test all the above assumptions by recording blood gas values in free-swimming tuna. We have developed techniques for capture, anaesthetization, instrumentation and recovery of tuna and for sampling dorsal and ventral aortic blood from animals swimming in a large doughnut-shaped tank. The results varied markedly from the above assumptions so we reinvestigated the blood gas properties of tuna blood and found, for kawakawa (*Euthynnus affinis*, Cantor), considerably different results from those obtained recently for bluefin (*T. thynnus*; Carey & Gibson, 1983) and albacore tuna (*T. alalunga*; Cech *et al.* 1984).

METHODS

Experiments were done on kawakawa, *Euthynnus affinis*, weighing from 0·9 to 2 kg, which were purchased from local commercial fishermen and maintained in outdoor tanks at 25 °C at the National Marine Fisheries Service Kewalo Research Facility.

For anaesthetization, a kawakawa was forced to swim into a plastic bag (complete method described in Kaya, Queenth & Dizon, 1984) containing oxygenated sea water and approximately $1\,\mathrm{g\,l^{-1}}$ of the water-soluble fish anaesthetic, tricaine methanesulphonate (MS-222). The capture bag was held underwater until the fish stopped struggling. The fish was then rushed into the laboratory and placed dorsal side up in a cradle formed by suspending chamois leather between a vertical pair of plastic supports. Oxygenated sea water, with $0{\cdot}07$–$0{\cdot}1\,\mathrm{g\,l^{-1}}$ MS-222 to maintain anaesthesia, was recirculated over the gills through a tube placed in the mouth.

Catheterization of the dorsal aorta was done using a modification of the method described by Smith & Bell (1967) for salmonids. The animal was turned ventral side up and the gills were irrigated by backflushing oxygenated sea water through the opercular openings. The mouth was held open by retractors and either an 18 or 20 gauge Teflon catheter (5 cm long) was inserted into the aorta using an intravenous catheter placement unit. The placement unit consists of a stainless steel needle and

hub, inside a Teflon catheter and hub. The catheter placement unit was filled with heparinized saline (10–30 i.u. ml^{-1}) and the inner steel needle was connected, *via* a coupling made from a 1-ml tuberculin syringe and a long length of saline-filled PE 160 tubing, to a blood pressure transducer. The needle and catheter were inserted through the skin at the point where the first gill arch joins the roof of the mouth (Fig. 1). To obtain the proper angle during insertion, the placement unit was then held approximately 0·5 cm medial to the 'V' formed on the side of the mouth by the premaxillary and dentary bones. The needle and catheter were then slowly pushed posteriorly until blood pressure was observed on a chart recorder. The needle hub was then held firmly and the catheter slid off the needle and advanced down the dorsal aorta. Blood pressure was carefully monitored at this time to ensure that the Teflon catheter remained in the blood vessel and that the tip did not become lodged against the vessel wall.

After the Teflon catheter had been advanced 2 or 3 cm down the dorsal aorta, the steel needle was quickly withdrawn and a male luer tip attached to a 1-m length of PE 160 tubing was inserted into the hub of the Teflon catheter. With practice this was performed with little blood loss. The catheter was then secured with a suture to the roof of the mouth and was brought out through the snout (Fig. 1) as described by Smith & Bell (1967).

It was necessary to enter the roof of the mouth at an angle, rather than in the midline, to avoid the large pharyngeal teeth overlying the dorsal aorta and bony knob projecting ventrally from the posterior end of the parasphenoid bone (see Gibbs & Collette, 1967, for a description of skeletal anatomy). An advantage of this procedure was that by positioning the placement unit near the 'V' formed by the premaxillary and dentary bones, an accurate angle for advancing the catheter was provided which ensured that the needle entered the aorta at the 'Y' formed by the combined efferent arteries from the first and second gill arches (Fig. 1).

The ventral aorta was also approached with the fish upside down. A placement unit was used to insert a Teflon catheter (18 or 20 gauge) approximately 1 cm anterior to the junction of the ventricle and bulbus arteriosus. This point was estimated using external markers as a guide. The body wall over the ventricle is stiff but over the extreme anterior end of the ventricle it becomes much more flexible. The placement unit was pushed through the skin in the midline, at a 45° angle to the body surface, approximately 0·5–1 cm anterior to the end of the stiff region of the body wall. The needle and catheter were advanced anteriorly until blood pressure was seen on the chart recorder. The needle was then held firmly and the Teflon catheter carefully advanced anteriorly along the ventral aorta. Once the catheter was in place, the needle was removed and a male luer connector on the end of PE 160 tubing plugged into the hub of the catheter. The whole system was then sutured to the body wall. At the conclusion of an experiment the location of the tips of the catheters in both dorsal and ventral aortae were checked *post mortem* (Fig. 1).

After catheterization, the animal was placed upright in the cradle and the catheters were sutured to the body wall just behind the dorsal fin. If recovery was to be effected the anaesthetic was slowly diluted until the animal started to make rhythmic body

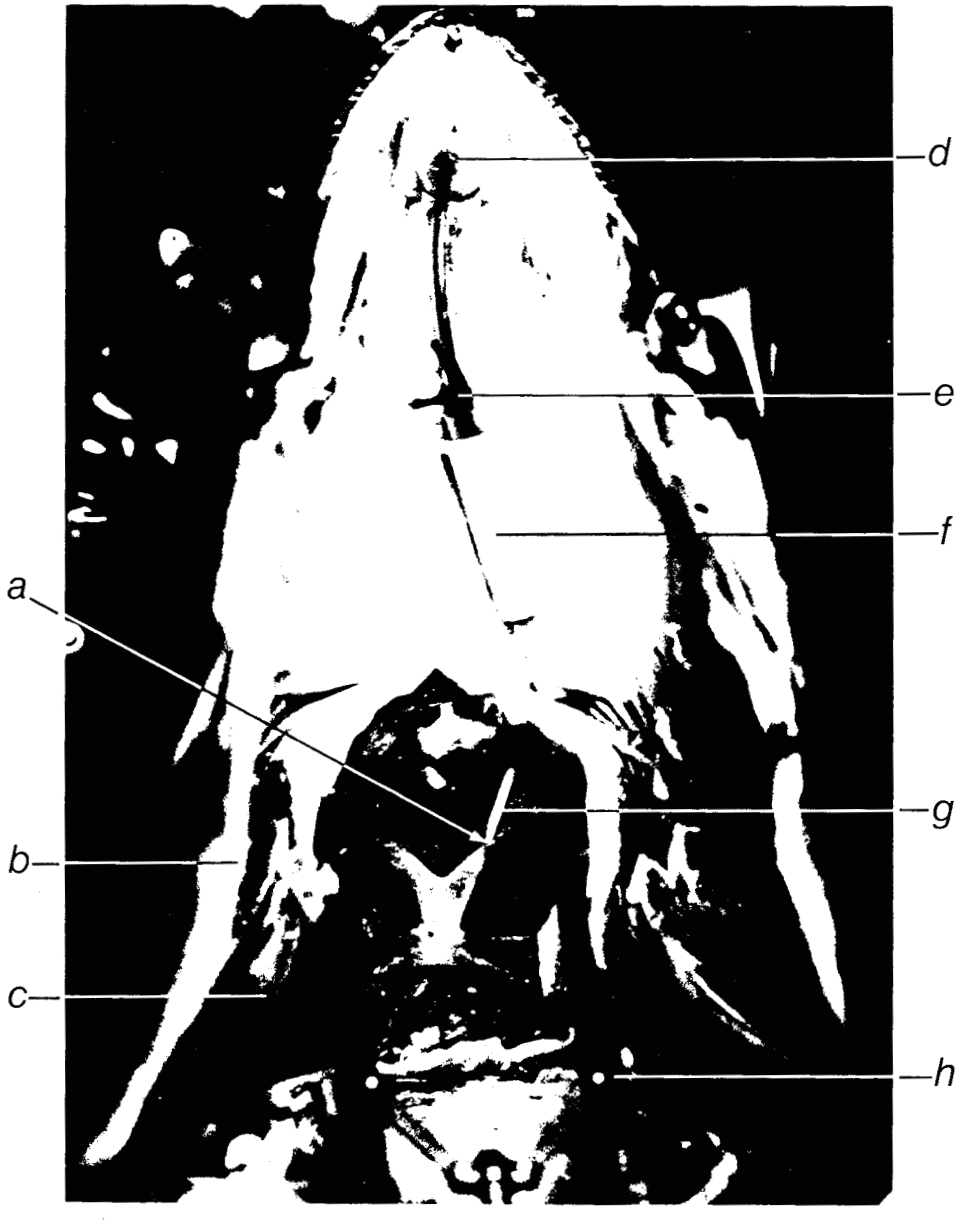

Fig. 1. Catheterization of the dorsal aorta in kawakawa, as revealed at *post mortem*. The lower jaw has been removed and the skin and muscle layers ventral to the dorsal aorta divided in the midline. The arrow shows the point of penetration into the efferent branchial artery. *a*, point of entry into gill artery; *b*, operculum; *c*, gills; *d*, flanged sleeve; *e*, tie to roof of mouth; *f*, catheter hub; *g*, Teflon catheter; *h*, retractors.

movements. Both catheters were plugged and the fish was rapidly transferred to a large doughnut-shaped tank (17·1 m i.d. and 17·8 m o.d.). Fresh sea water was pumped over the gills until the fish was able to swim on its own. Some fish swam laps of the tank and it was possible to get a fairly accurate assessment of swimming speed from these animals. Blood samples were taken simultaneously into syringes attached to the catheters, by an operator who ran around the tank keeping pace with the fish. After sampling, the catheters were flushed with heparinized saline and replugged. Survival was not good. Fish with dorsal and ventral aortic catheters succumbed within 3 h after the start of swimming. In three fish we only implanted a dorsal aortic catheter and these fish survived much longer, but all three died by 18 h after the end of the surgery. We are not sure whether the longer survival was due to less surgery or a decrease in the effort required to pull one cannula instead of two.

Other fish were not allowed to recover from anaesthesia. These animals were placed in a Perspex box, dorsal side up in the cradle, and were force-ventilated from a pump. A light level of anaesthesia was maintained throughout. The majority of these fish had only one catheter, located in either the dorsal or ventral aorta. Blood samples were taken from these fish and were used to construct O_2- and CO_2-combining curves.

Aliquots of blood (3–5 ml) were placed in tonometers (50 ml) which were shaken at 25 °C in a constant temperature bath. The blood was equilibrated for 20 min, a time found to be adequate, with humidified gases obtained from a gas mixing pump (Wösthoff, Bochum, W. Germany). Various mixtures of $P_{CO_2} = 0$, 2·54, 5·07, 11·5, 30·5 or 61·3 mmHg were made in both air and nitrogen and were stored in rubber tyres. P_{CO_2} tension was the same in a pair of tonometers. Blood samples were taken from each tonometer (one equilibrated with air + CO_2 and the other with N_2 + CO_2) and oxygen and carbon dioxide concentrations were determined using the methods of Tucker (1967) and Cameron (1971). The Tucker (1967) method was modified somewhat in that we used 100 μl of distilled water, equilibrated with pure oxygen at 25 °C, as a reference sample for determining oxygen concentration in 25 μl of whole blood. The cuvettes containing the oxygen and CO_2 electrodes were maintained at 40 °C to improve the response time of the electrodes and accuracy of the determinations. All solutions were also held at this temperature except the 100 % oxygenated distilled water. The P_{O_2} of this water, which was used as the reference sample, was measured using a Radiometer oxygen electrode at 25 °C. Oxygen equilibration curves were constructed using the mixing method (Haab, Piiper & Rahn, 1960; Edwards & Martin, 1966) but incorporating improvements suggested by Scheid & Meyer (1978). Haematocrits of the blood in the tonometers and of each sample after mixing were determined in duplicate. No haemolysis occurred, judging from the colour of the plasma in the haematocrit tube after centrifugation. Some blood was tonometered for long periods to determine if P_{50} changed with time. After 75 min of tonometry, P_{50} was the same as was obtained after 20 min. Eleven oxygen dissociation curves were constructed using the blood from five tuna at P_{CO_2} from 0 to 11·5 mmHg and 32 determinations of P_{50} were made on blood from nine fish. The presence of a Root effect means that at a given P_{O_2} blood will carry less oxygen as the

P_{CO_2} increases. Hence, in fish blood, the P_{50} obtained at various P_{CO_2} levels does not represent similar concentrations of oxygen. As this reflects the situation *in vivo*, no attempt was made to correct values from the mixing method for the Root effect. CO_2-combining curves were constructed also using the blood from six fish; the blood of two of these had been used in determinations of oxygen-combining properties. The Root effect was measured in blood from six fish, although each fish was used for only a single determination.

Blood gas tensions and pH were measured using Radiometer electrodes, in cuvettes thermostatted at 25°C, and connected to Radiometer PHM 71 Mk 2 or Radiometer PHM 73 gas monitors. The pH electrode was calibrated using precision buffer solutions and the gas electrodes with mixtures obtained from the gas mixing pump, although the zero calibration on the oxygen electrode was checked periodically using an alkaline sulphite solution (S4150, Radiometer, Copenhagen). The environmental temperature of the kawakawa was 25°C so as to simulate the effects of the blood being warmed in the retial system, dorsal aortic blood samples, from three fish, were drawn into glass syringes and injected into cuvettes held at 35°C and analysed in a blood gas system maintained and calibrated at 35°C. A stable reading was obtained after 2 min. The values for the warmed blood were compared with values obtained at 25°C using freshly drawn blood analysed in the blood gas system held and calibrated at 25°C.

In the text, all values are given as means ± one S.E.M.,(N), where N = number of observations. Regression analyses were performed on a computer using the data analysis package, 'S', for UNIX operating systems (Becker & Chambers, 1984).

RESULTS

In vivo *observations*

Blood gas values and pH of blood from tuna swimming at speeds from 1·8 to 2·9 body lengths s^{-1} are given in Table 1. Dorsal aortic blood was always more alkaline than ventral aortic blood although in one case the difference was quite small (tuna no. 1, Table 1). Nevertheless, this contrasts with our extrapolation of Cech *et al.*'s (1984) data which indicated that dorsal aortic blood would be more acid than ventral aortic blood. Ventral aortic P_{O_2} never exceeded 16 mmHg, while dorsal aortic P_{O_2} was always below 100 mmHg and in two of the three tuna that only had a dorsal aortic cannula and survived 18 h post-operatively, dorsal aortic P_{O_2} was below 42 mmHg (tuna nos 7 and 8, Table 1). P_{CO_2} in the dorsal aorta varied from 3·7 to 7 mmHg but there was no apparent relationship between dorsal aortic P_{O_2} and P_{CO_2}.

Warming dorsal aortic blood sampled from three free-swimming kawakawa by 10°C, from 25 to 35°C in a closed system, caused P_{O_2} to increase by 25 % ± 14 % (9) and P_{CO_2} to more than double [increase = 105·7 % ± 6·4 % (9)]. The P_{O_2} of the freshly sampled blood varied from 40 to 102 mmHg at 25°C and P_{CO_2} varied from 2·9 to 5·1 mmHg. Dorsal aortic blood pH fell by, on average, 0·15 ± 0·01 (9) units when blood was warmed by 10°C.

Table 1. *Blood gas tensions and pH in blood sampled from free-swimming tuna* Euthynnus affinis

	Ventral aorta						Dorsal aorta			
Tuna no.	P_{O_2} (mmHg)	P_{CO_2} (mmHg)	pH	Hct (%)	Fork length (cm)	Swimming speed (body lengths s^{-1})	P_{O_2} (mmHg)	P_{CO_2} (mmHg)	pH	Hct (%)
1	14	8·9	7·57	29	43	SNR	56·4	5·2	7·59	29
2	16	5·8	7·68	—	42	SNR	—	—	—	
3	12·7	10·7	7·66	28	37·5	2·9	68·7	7	7·80	24
4	11·7	8·6	7·70	42	45	1·8	67·4	5·4	7·76	35
5	8·5	8·9	7·61	44	44	2·27	44·6	6·9	7·68	39
6	12	7·3	7·73	32	47	1·8	91·7	4·2	7·8	34
7	—	—	—	—	37	SNR	41·7	4·1	7·74	36
8	—	—	—	—	36	SNR	34·5	4·2	7·83	43
9	—	—	—	—	38	SNR	88	4·7	—	28
10	12·5	6·2	7·60	37	37	SNR	52	3·7	7·76	37
	12·5 ± 0·9 (7)	8·07 ± 0·65 (7)	7·65 ± 0·02 (7)	35·3 ± 2·75 (6)			62·7 ± 5·92 (9)	5·05 ± 0·4 (9)	7·77 ± 0·04 (8)	33·8 ± 1·97 (9)

SNR = fish swimming but speed not recorded.
Number of fish given in brackets.

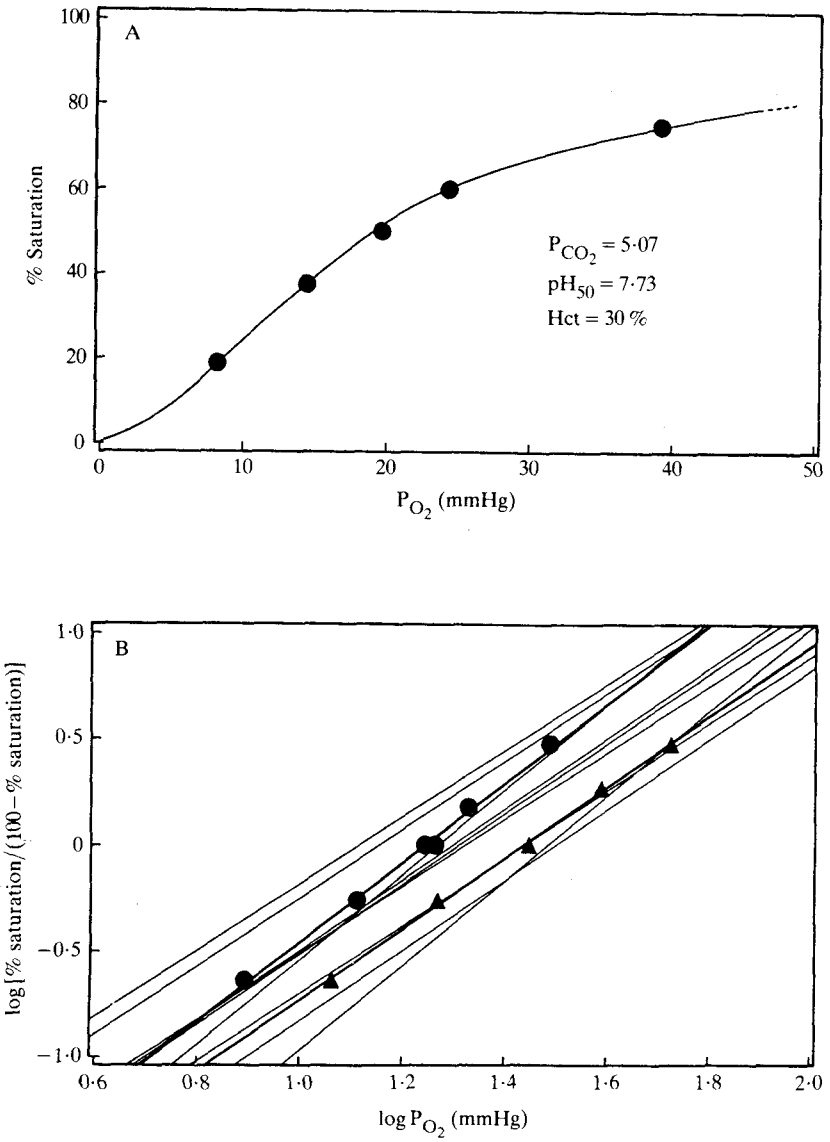

Fig. 2. (A) A blood oxygen dissociation curve of kawakawa whole blood (Hct = 30 %) at 25 °C and pH_{50} = 7·73. The blood was equilibrated with gas mixtures containing 5·04 mmHg P_{CO_2}. The curve was fitted by eye. (B) Hill's plots of the 11 oxygen dissociation curves determined in this study. Data points are only shown for the two heavy regression lines.

In vitro *observations*

Oxygen-combining properties of kawakawa blood

Dissociation curves for the blood were sigmoid (Fig. 2A) with a mean Hill's number of 1·72 ± 0·05 for the eleven determinations (Fig. 2B). Hill's numbers

varied from 1·57 to 2·0 over a pH range (at the P_{50}) of 7 to 8, but there was no relationship between the value of Hill's number and pH. At full saturation, oxygen concentration in the blood varied with haematocrit. This relationship is expressed by the equation:

$$\text{Oxygen (mmol l}^{-1}) = -0{\cdot}7+0{\cdot}27\,\text{Hct\%}\ (r^2 = 0{\cdot}76).$$

P_{50} increased with a decrease in pH of the blood, caused by changing P_{CO_2}, from 10·1 mmHg at pH = 7·95 to 41·5 mmHg at pH = 7·13. Over the range of pH values encountered in free-swimming tuna (pH 7·57–7·83), the P_{50} varied from 30·9 to 13·7 mmHg, with an average value of 21 ± 1·75 mmHg (8). The oxygen concentration of the blood fell (Root effect) with an increase in P_{CO_2} from 0 to 61·3 mmHg, by $-0{\cdot}64 \pm 0{\cdot}1$ % mmHg $P_{CO_2}^{-1}$ (6) ($r^2 = 0{\cdot}9$), where the oxygen concentration at $P_{CO_2} = 0$ mmHg was taken as 100 %.

The Bohr coefficient, obtained from a plot of log P_{50} *versus* pH, was $-0{\cdot}59 \pm 0{\cdot}046$ (30) ($r^2 = 0{\cdot}85$) (Fig. 3). The Bohr coefficient increased to $-0{\cdot}83 \pm 0{\cdot}23$ (10) ($r^2 = 0{\cdot}61$) over the more restricted pH range from 7·55 to 7·85, which encompassed the pH values obtained in free-swimming animals.

Blood from a single fish which struggled violently just before sampling had a pH around 7 even after 20 min equilibration with a gas mixture without CO_2. Two determinations of P_{50} on this blood fell considerably below the line describing the CO_2-induced Bohr effect (▲ in Fig. 3). Unfortunately, lactate concentration was not measured but if the low pH was due to lactacidosis then these data indicate that CO_2-induced and metabolic acid-induced Bohr coefficients could be different.

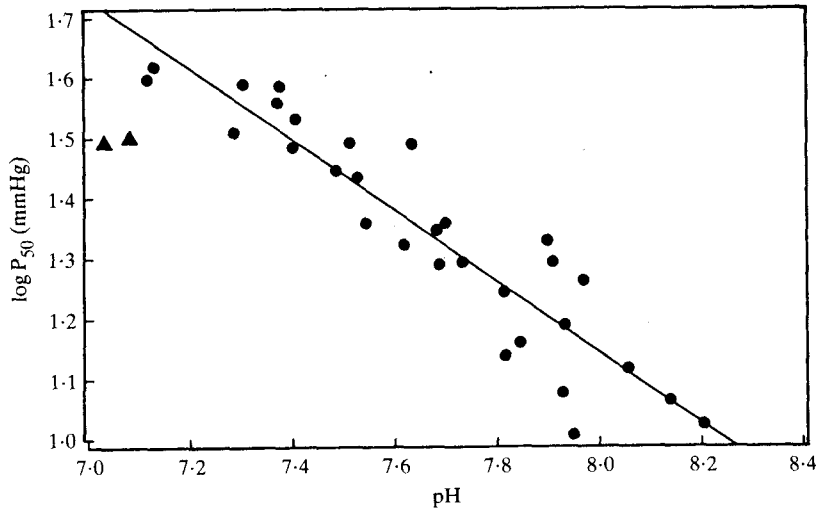

Fig. 3. Plot of logP_{50} *versus* pH for determining the CO_2-induced Bohr coefficient of kawakawa whole blood at 25 °C. Two points (▲) were obtained from blood in which pH was low even though the equilibrating gas was without CO_2. These points were not included in determining the CO_2-induced Bohr coefficient.

Carbon dioxide-combining properties of kawakawa blood

The relationship between P_{CO_2} and CO_2 concentration for whole blood, with haematocrits in the range from 29 to 36% (average 31·5%), is shown in Fig. 4A. At any given level of P_{CO_2}, deoxygenated blood had a higher concentration of CO_2 than oxygenated blood, although the difference in concentration was unchanged over a P_{CO_2} range from 2·5 to 30·5 mmHg. A 'buffer curve' was obtained by plotting the relationship between pH and logP_{CO_2} for blood samples with haematocrits from 25 to 35% (Fig. 4B). The slope of the relationship for deoxygenated blood [$-0{\cdot}611 \pm 0{\cdot}04$ (9) ($r^2 = 0{\cdot}97$)] appeared steeper than that for oxygenated blood [$-0{\cdot}5 \pm 0{\cdot}04$ (9) ($r^2 = 0{\cdot}96$)], but the difference between the slopes was not significant at the 5% level.

DISCUSSION

Predicted values of blood gas tensions in dorsal and ventral aortae of tuna based on published values of blood gas chemistry are at variance with our measurements in free-swimming kawakawa. Apart from errors in measurement or interpretation, the only possibility which could explain these discrepancies is marked interspecific variations in the oxygen- and CO_2-combining properties of tuna blood. In this respect, our recordings of oxygen- and CO_2-combining properties of kawakawa blood substantiate the measurements we obtained from free-swimming fish. For instance, the Bohr coefficient is less than $-0{\cdot}6$ and in every instance dorsal aortic pH was more alkaline than that in the ventral aorta. Ventral aortic P_{O_2} was, on average, 12·5 mmHg, which was well below the mean value for P_{50} observed over the range of pH encountered in free-swimming fish.

Dorsal aortic P_{CO_2} was high and, in fact, is perhaps the highest yet reported for free-swimming teleosts (Stevens & Randall, 1967; Holeton, Pawson & Shelton, 1982; Boutilier, Aughton & Shelton, 1984). The high arterial P_{CO_2} may explain, in part, why no reverse temperature effect on blood oxygen dissociation was observed when dorsal aortic blood was warmed from 25 to 35°C. Even so, a much reduced reverse temperature effect was expected because Cech *et al.* (1984) reported that the effect is diminished and reverts to a more typical form between 30 and 35°C in albacore blood. In their environment and in the holding tanks, our tuna can live quite happily in the absence of any advantage conferred by reversed thermal effects. It may be that the low dorsal aortic P_{O_2} observed in free-swimming animals renders this effect unnecessary or, more likely, that the claimed advantage of this effect in ensuring adequate muscle oxygenation has been overstated (see Carey & Gibson, 1983).

In most vertebrate bloods there is a difference in CO_2 concentration between oxygenated and deoxygenated blood, at a given P_{CO_2}. This difference increases with increasing P_{CO_2}. Also, deoxygenated blood is more alkaline than oxygenated blood at any given P_{CO_2}, and this pH difference is constant over a wide range of P_{CO_2} values. These differences are a reflection of changes in the properties of haemoglobin on oxygenation or deoxygenation. Hence, the CO_2-combining properties of kawakawa blood are unusual in that the CO_2 concentration difference between oxygenated and

deoxygenated blood does not increase with P_{CO_2} while the pH difference is reduced with increasing P_{CO_2}. As these differences are dependent on oxygen combining with haemoglobin, the unusual properties of kawakawa blood are probably the result of the Root effect.

Our method of looking at the buffering properties of tuna blood should also be mentioned. In the light of recent quantitative analyses of acid–base balance

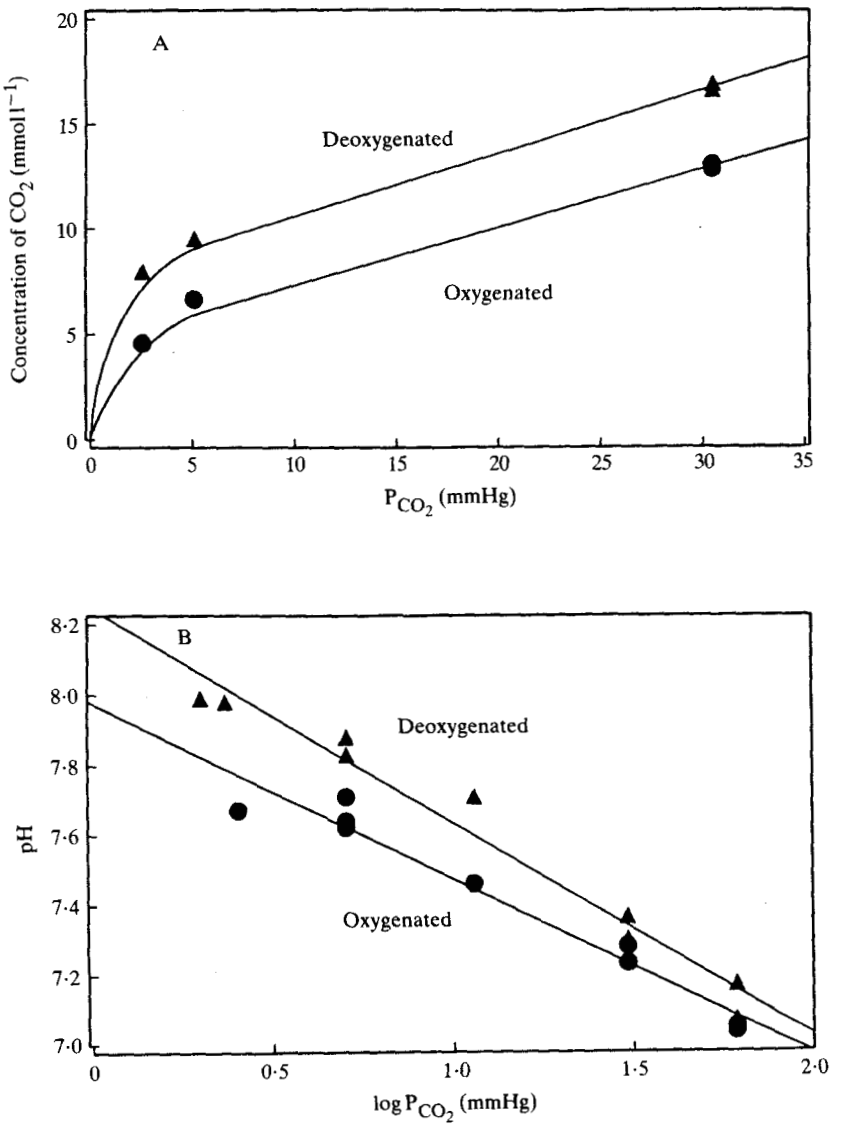

Fig. 4. (A) CO_2-combining curve for air-saturated and deoxygenated blood of kawakawa at 25 °C. Curves fitted by eye. (B) 'Buffer curves' of air-saturated and deoxygenated kawakawa whole blood displayed as the relationship between pH and log P_{CO_2}.

(Stewart, 1983) it seems more rational to analyse buffer properties with the independent variable (P_{CO_2}) on the abscissa rather than the ordinate. The slope of the relationship, pH *versus* $\log P_{CO_2}$, for tuna blood falls between −0·5 (oxygenated) and −0·61 (deoxygenated) which is in the same range as values obtained from elasmobranchs and other teleosts (Albers & Pleschka, 1967; Cameron & Randall, 1972; Root, 1931; Weber, Wells & Rossetti, 1983).

In the pH range 7 to 8 we found that the variation in Hill's number, from 1·57 to 2·0, was not related to pH. Hill's equation is theoretically incorrect, and is usually replaced by the Adair intermediate compound equation, but it is still a convenient and useful way to compare physiological data. Given the above proviso, the value for Hill's number of 1·1 obtained by Cech *et al.* (1984) for albacore blood is strikingly different from that for kawakawa blood. Finding a hyperbolic blood curve (Hill's number = 1) in an extremely active and highly aerobic animal like tuna is quite unexpected. Tuna are warm-bodied and are claimed to consume oxygen at the same rate as similarly sized mammals (Stevens & Carey, 1981), so a sigmoid dissociation curve would be expected (Haldane & Priestley, 1935; Riggs, 1970) and this has been confirmed by the present observations on kawakawa.

A theoretical analysis based on morphometric observations of the gills (Hughes, 1978, 1984) and estimates of gill water flow (Stevens, 1972), suggests that P_{CO_2} in dorsal aortic blood of tuna will be low (Rahn, 1966). Obviously this was not the case (Table 1). The fact that dorsal aortic P_{O_2} was also low implies that, at least at swimming speeds of 1·8–3 body lengths s^{-1}, efficacy of gas transfer is compromised. Certainly it would be most valuable to obtain data from tuna swimming at higher speeds; observations on the scombrid, *Scomber scombrus*, indicate that dorsal aortic P_{CO_2} falls when swimming speed increases (Boutilier *et al.* 1984). The fall in P_{CO_2} serves to minimize the effects of increasing lactacidosis on dorsal aortic pH. Whether dorsal aortic P_{O_2} would increase and P_{CO_2} fall at higher swimming speeds in tuna is not known but it is an interesting avenue for future research.

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