

O₂ tension, swimming-velocity, and thermal effects on the metabolic rate of the Pacific albacore *Thunnus alalunga*

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Summary. The oxygen consumption rates ($\dot{V}O_2$) of 9 albacore tuna, *Thunnus alalunga* (8.5–12 kg) were measured at sea in a swimming respirometer to determine the effects of relative swimming velocity, ambient O₂ tension, and water temperature. Significant positive relationships were obtained between tail-beat frequency and relative speed and between relative speed and $\dot{V}O_2$. The albacore metabolic rate was not appreciably affected by exposure to water temperatures ranging from 13.5° to 16.9°C. Brief exposure to hyperoxia (200–400 mmHg), which was done to reduce the initial stress upon fish in the respirometer, did not affect $\dot{V}O_2$. Hypoxia (50–99 mmHg), however, did tend to reduce $\dot{V}O_2$ and affect swimming velocity.

Key words: *Thunnus alalunga* – Tuna – Oxygen consumption – Swimming metabolism

Introduction

The strength and metabolic requirements of tunas pose logistically difficult problems for in vivo and respirometry studies. However, the last few years have witnessed steady progress toward the objective of maintaining tunas in viable condition while controlled physiological experiments are carried out. Recent studies have examined aspects of the acid-base physiology (Perry et al. 1985a, b) and the blood gas parameters (Jones et al. 1986) of swimming skipjack. A major contribution to the study of tuna physiology has been made by the United States National Oceanographic and Atmospheric Administration's R.V. *David Starr Jordan* which, between 1977 and 1985, was used

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for physiological, behavioural, and ecological studies on the Pacific albacore *Thunnus alalunga* (Bonnaterre).

Physiological studies with the albacore have demonstrated that it has a large blood volume (Laurs et al. 1978), thermoregulates in cool water (Graham and Dickson 1981), has a metabolic rate close to that of a mammal (Graham and Laurs 1982), exhibits a reversed temperature effect for haemoglobin-O₂ binding that is in turn integrated with its elevated body temperature (Cech et al. 1984; White et al. 1988), and has a high blood pressure and cardiac output, as well as a negative pericardial pressure (Breisch et al. 1983; Lai et al. 1987; White et al. 1988).

The first metabolic measurements reported for *T. alalunga* (Graham and Laurs 1982) were made at sea with a respirometer that did not have elaborate thermal, ambient O₂, or water velocity control capabilities. In studies carried out aboard the *Jordan* in 1985 an improved water tunnel design was used, and we report here on the combined and separate effects of water O₂ tension, temperature, and swimming velocity, as well as the influence of the time since capture on the O₂ consumption rate ($\dot{V}O_2$) of the Pacific albacore. Such studies will improve our understanding of albacore physiology, and reveal environmental factors that are likely to determine the short-term movement patterns of migrating schools. This in turn may lead to the more efficient harvest and management of this important fishery species.

Materials and methods

Studies were carried out in August 1985, using albacore collected off Monterey, California (USA) where sea surface temperatures ranged from 15.8° to 17.0°C. Fish were caught by

trolling and handled as described by Graham and Laurs (1982), Lai et al. (1987) and White et al. (1988). Fish not seriously injured by the hook were quickly transferred to the chilled (about 15°C), oxygenated, and flowing water in a 470 l swimming respirometer.

The respirometer, similar to the water channel described by Prange (1976), consisted of a closed loop of flowing water, separated horizontally, and connected at each end by curved metal vanes. The respirometer working section (113 × 30 × 29 cm) was contained in the upper horizontal channel. A lucite cover containing a removable hatch was sealed over the upper channel and working section by a neoprene gasket. The hatch was opened to introduce and remove the fish. A standpipe was used to add water. This pipe and bent tubes in each corner of the top were used to purge air from the chamber.

Water was driven around the system by a three quarter hp variable speed motor (Minarik Blue Chip II) mounted outside the lower channel, and coupled to the propeller shaft which entered the respirometer through sealed bearings. Honeycomb collimator material, at both ends of the working section, confined the fish and smoothed the flow. Rectilinear flow through the working section was verified by observation of moving particles. The maximum velocity of the respirometer in this configuration is about 1.25 m/s. Velocities were calibrated by a flow meter (General Oceanics, Model 2035-mk III). Because of the solid blocking effects induced by the cross-sectional area of the fish body, working section velocities were corrected as described by Graham and Laurs (1982).

To control temperature and maintain clean water during tests, respirometer water was pumped through a heat-exchanging and filtration circuit. Prior to most studies, respirometer water was chilled to 14°–15°C, which is within the range normally encountered by albacore swimming below the mixed layer (Laurs and Lynn 1977; Laurs et al. 1980). Tanks of compressed O₂ were used to elevate respirometer O₂ tension. Earlier studies (Graham and Dickson 1981; Graham and Laurs 1982) suggested that this relieved stress, and enabled albacore to recover more quickly from the shocks of capture and handling, and adjust to confinement in the respirometer.

A Yellow Springs O₂ and temperature meter (Model 54A) and probe (5450/5750) were used to monitor temperature and O₂ tension in the respirometer. The O₂ electrode had been standardized with air and N₂ gas, and was regularly calibrated in air during the tests. A voltage-controlled reciprocating pump circulated respirometer water from the system, through the probe housing and back again.

A fish was placed in the system, and observed prior to respirometry measurements to verify that it swam regularly. The anterior third of the working section was painted black in order to calm the fish, and provide orientation marks for maintaining station, and the front end of the section was always covered with a black cloth during swimming studies. Depending upon fish performance and condition, the total time that fish were maintained in the respirometer ranged from 177 to 553 min. The time interval that passed before respirometry began, varied between 14 and 119 min. Two to eight replicate VO₂ measurements were made on each albacore. For this, the respirometer was sealed for a specific time, and the decline in PO₂ recorded. Then the system was opened, the O₂ level raised, and the process repeated. During each run the water velocity was continuously adjusted so that the fish swam steadily. In addition to O₂, temperature, and velocity, fish tail-beat frequency was recorded at regular intervals during each run. After tests were completed the fish was removed and its mass and fork length (L) determined. The final fish tested (no. 11) was in such excellent condition at the end of the tests that it was released.

Calculations of VO₂ were based on the net (background corrected) reduction rate of ambient O₂. Data were reduced to mean instantaneous VO₂ estimates, based on small increments of PO₂ change, and the mean values of other recorded variables over the same period. These were then delineated, for interfish comparison, on the basis of temperature (± 1°C) and PO₂ range (either ± 100 or ± 50 mmHg) in the respirometer, relative swimming speed (L/s), and tail-beat frequency (Hz). All regression equations were tested for a significant ($P < 0.05$) slope by *t*-test.

Results and Discussion

Data were obtained for 9 albacore (8.5–12.0 kg) swimming at various combinations of temperature (13.5°–18.0°C), O₂ tensions (ranging from 50–440 mmHg, normoxia = 150 mmHg) and speed (0.5–1.4 L/s). Our experimental protocol and the form of data acquisition are illustrated for albacore no. 8 which was used in 3 VO₂ runs (Table 1). Run 1 began after a 79 min habituation period, and the fish swam in the respirometer for 6.1 h. All runs began in high ambient PO₂ which decreased with time. Table 1 indicates that the performance of fish no. 8 improved with time since capture. At first this fish would not swim and for most of the first 3 h, it swam irregularly and had a low VO₂. By the third run, both its VO₂ and velocity were elevated. Tables 2 and 3 contain summary data for albacore nos. 5 and 11. These tables have the same format as Table 1, except that VO₂ is reported for the entire run rather than smaller PO₂ regimes. As with fish no. 8, albacore nos. 5 and 11 also seemed to gain strength with time. This may be a "training" effect, or may indicate the fishes' recovery from the rigours of capture and handling.

It was found that differences in fish body size and physiological state following capture, often established a narrow range of swimming speeds; pooled data for all fish in all combinations of PO₂ range, temperature, and speed (Fig. 1) demonstrate this. Fig. 1A shows the significant linear relationship between tail-beat frequency and relative velocity determined for all fish under all experimental conditions. Inspection of these data, however, reveals that tail-beat frequencies for the lowest PO₂ range (dots, Fig. 1A) occur consistently at higher velocities, suggesting that low PO₂ – possibly by affecting caudal amplitude – alters the relationship between albacore tail-beat frequency and swimming speed. The ratio of speed to tail-beat (stride length) for albacore (0.5–0.6) is similar to that of other scombrids over this velocity range (Magnuson 1978). The significant relationship between swimming velocity and VO₂ (Fig. 1B) is not affected by high PO₂. It can be seen, however, that

Table 1. Records of mean water temperature, tail-beat frequency, swimming speed, and instantaneous $\dot{V}O_2$ of albacore no. 8 (11.0 kg) during 3 respirometry runs. Note that respirometer PO_2 declines during each run. Time intervals indicate duration of each run and the time before and between each run. Total elapsed test time was 6.1 h

	Run 1					Run 2				Run 3						
	79 min	104 min				27 min	71 min			38 min	49 min					
PO_2		400	299	199	149	99		400	299	199	149		400	299	199	149
		-300	-200	-150	-100	-50		-300	-200	-150	-100		-300	-200	-150	-100
$^{\circ}C$	\bar{x}	14.6	14.1	14.1	14.7	14.7		15.0	14.9	14.8	14.8		15.2	15.2	15.2	15.2
		± 0.1	± 0	± 0.1	± 0	± 0		± 0	± 0	± 0	± 0		± 0	± 0	± 0	± 0
	<i>n</i>	10	15	8	10	8		7	21	7	9		7	10	4	3
Tail beat ^a	\bar{x}	1.86	1.91	1.92	1.93	1.94		2.28	2.17	2.11	2.11		2.37	2.14	2.17	2.14
(Hz)	<i>n</i>	8	11	7	5	6		6	5	6	8		4	7	2	3
U^b (L/s)	\bar{x}	0.74	0.93	1.01	1.11	1.19		1.10	1.11	1.15	1.23		1.00	1.06	1.11	1.11
	<i>n</i>	10	15	8	10	8		7	21	7	9		7	4	4	3
$\dot{V}O_2$	\bar{x}	57.0	37.9	39.3	37.5	43.1		56.0	68.9	52.4	41.6		63.9	66.3	65.3	66.6
(ml/min)		± 15	± 3	± 4	± 3	± 8		± 5	± 16	± 5	± 7		± 3	± 1	± 1	± 5
	<i>n</i>	10	15	8	10	8		6	17	7	8		6	10	4	3

^a All SE value < 0.1

^b All SE values ≤ 0.01

Table 2. Summary data for the 8 $\dot{V}O_2$ runs made on albacore no. 5 (11.5 kg). Data presentation is similar to Table 1 except that $\dot{V}O_2$ data are combined for the entire PO_2 range. Total duration of study, 9.2 h

Pre-run Interval (min)	50	17	32	36	26	17	11	13
Run no.	1	2	3	4	5	6	7	8
Duration (min)	62	17	26	41	99	22	35	48
$^{\circ}C$	14.9	15.4	15.8	16.8	16.5	16.2	15.0	15.5
PO_2 range (torr)	312-112	160-107	200-114	181-62	400-52	184-75	150-60	240-140
Tailbeat ^a (\bar{x}) (Hz)	2.0	2.0	1.9	1.8	1.7	1.8	1.8	1.9
U^b (\bar{x}) (L/s)	0.53	0.63	0.72	0.72	0.73	0.82	0.86	0.80
$\dot{V}O_2$ \bar{x} (SE), ml/min	41 (2)	43 (9)	40 (5)	34 (4)	41 (3)	49 (5)	46 (4)	52 (3)

^a All SE values ≤ 0.06

^b All SE values ≤ 0.02

Table 3. Summary data for the 6 $\dot{V}O_2$ runs made for albacore no. 11 (8.5 kg). See text and Table 2 for details. Total duration of study, 6.7 h

Pre-run Interval (min)	21	21	16	19	16	55
Run no.	1	2	3	4	5	6
Duration (min)	20	19	45	64	53	50
$^{\circ}C$	15.6	14.9	14.5	14.4	14.9	18.0
PO_2 range (torr)	195-111	172-108	214-78	305-104	335-124	380-59
Tailbeat ^a (\bar{x}) (Hz)	1.8	1.8	1.9	2.0	2.1	2.5
U^b (\bar{x}) (L/s)	0.60	0.63	0.77	0.95	1.0	1.0
$\dot{V}O_2$ \bar{x} (SE), ml/min	55 (6)	43 (4)	37 (2)	42 (2)	57 (4)	101 (9)

^a SE ≤ 0.06

^b SE ≤ 0.02

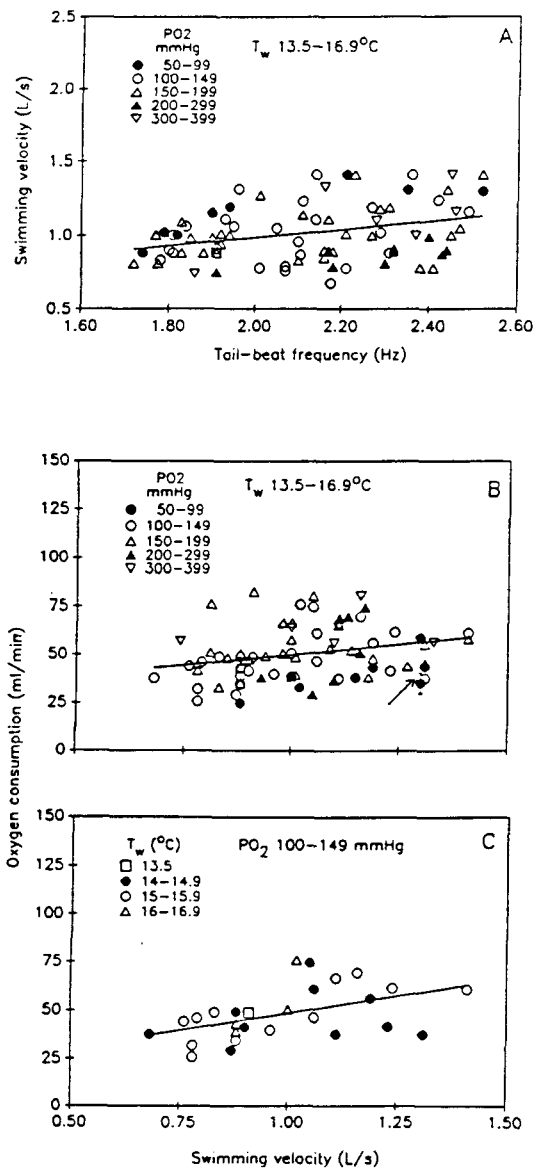


Fig. 1A. Effect of tail-beat frequency on the velocity of swimming albacore ($n = 9$) over a PO_2 range of 50–399 mmHg and water temperatures from 13.5° to 16.9°C. Equation for the significant ($P < 0.05$, t -test) regression line is $U = 0.43 + 0.28f$, where U = swimming velocity (L/s) and f = tail-beat frequency (Hz); $n = 81$. B. Effect of swimming velocity on the $\dot{V}O_2$ of albacore ($n = 9$). PO_2 and temperature ranges as in A. Equation for the significant regression is $\dot{V}O_2 = 28.5 + 21.5U$; $n = 77$. Value indicated by arrow is mean $\dot{V}O_2$, determined by Graham and Laurs (1982). C. $\dot{V}O_2$ -swimming velocity data obtained for 9 albacore at 13.5°–16.9°C and within the PO_2 range of 100–149 mmHg. Equation for the significant regression is $\dot{V}O_2 = 5.9 + 43.3U$; $n = 28$.

the $\dot{V}O_2$'s measured over the 50–99 mmHg range (dots, Fig. 1B) are consistently low compared to all other PO_2 ranges, suggesting a critical O_2 tension for albacore within this range (see below).

Figure 1C shows the $\dot{V}O_2$ -velocity data obtained for albacore both at the range of temperatures (13.5°–16.9°C) and within a PO_2 range (100–149 mmHg) that they would naturally encounter. This reveals that at slow velocities, and in O_2 tensions typically experienced by this species, a doubling of the relative velocity (from 0.7 to 1.4 L/s) results in a near doubling of its $\dot{V}O_2$. This increment of $\dot{V}O_2$ increase is similar to that measured for other species at slow speeds (*Salmo gairdneri* [Webb 1971]; *Oncorhynchus nerka* [Brett and Glass 1973]; *Seriola quinqueradiata* [Tsukamoto and Chiba 1981]). The $\dot{V}O_2$ values measured for albacore at a range of speeds in this study also agree (Fig. 1C) with that determined at one speed and a temperature range of 15°–19°C by Graham and Laurs (1982), of 35.6 ml/min at 1.3 L/s. Finally, extrapolation of the velocity- $\dot{V}O_2$ data in Fig. 1C to "zero" L/s yields a "resting" $\dot{V}O_2$ of 12.8 ml/min. This is similar to the total standard (non-swimming) metabolic rates estimated for 10 kg individuals (at 25°C) of 3 tuna species, using regression equations provided by Brill (1987): yellowfin $\dot{V}O_2$, 12.5 ml/min, skipjack 17.6 ml/min, Kawakawa, 14.4 ml/min.

The findings demonstrate that albacore $\dot{V}O_2$ is affected by swimming speed and PO_2 , as well as the time since fish capture. But our data do not show a significant mass effect, or an effect of temperature variations between 13.5° and 16.9°C (Fig. 1C) on the $\dot{V}O_2$ of this species. Thus, additional data are required. Yet, it is possible to analyse such multivariate data in order to identify other important determinants of albacore $\dot{V}O_2$. One procedure is to focus on the latter runs of each fish to lessen the "time since capture" variable. Figure 2A does this for fish no. 5, presenting only the $\dot{V}O_2$ data determined for runs 4–8. This again shows the slight effects of speed and water temperature on $\dot{V}O_2$, and the tendency for $\dot{V}O_2$ to decline at a PO_2 below 100 mmHg. Figure 2B contains data for runs 4, 5, and 6 of fish no. 11 and indicates good agreement for the $\dot{V}O_2$ of this fish during runs 4 and 5 (14.4° and 14.9°C) and that of fish no. 5. However, run 6, done at 18°C and with the fish swimming faster, shows a much higher $\dot{V}O_2$ that declines steadily with PO_2 . Over the ambient range of 100–149 mmHg, the $\dot{V}O_2$ during run 6 is 1.8 times higher than the mean rate at cooler temperatures (83 vs 49 ml/min, Fig. 2B), and the Q_{10} for this difference is 4.5.

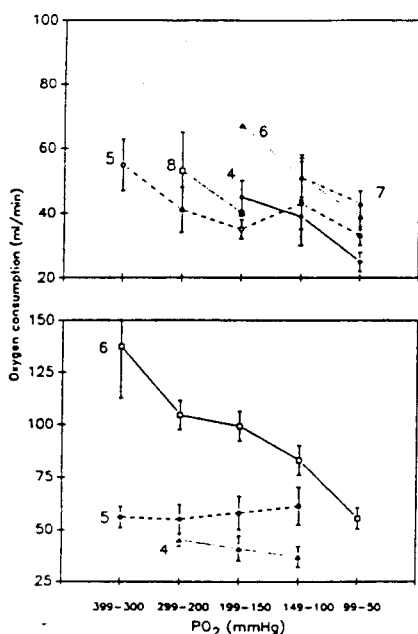


Fig. 2A. The $\dot{V}O_2$ ($\bar{x} \pm SE$) of albacore no. 5 as a function of PO_2 during runs 4, 5, 6, 7, and 8. The mean water temperature and fish swimming velocity during each run are: run 4 (16.8°C, 0.72 L/s), run 5 (16.4°C, 0.76 L/s), run 6 (16.2°C, 0.82 L/s), run 7 (15.0°C, 0.87 L/s), and run 8 (15.5°C, 0.80 L/s). The hours after capture at which each run began are run 4 (4.7 h), run 5 (5.1 h), run 6 (7 h), run 7 (7.6 h), and run 8 (8.4 h). B. The $\dot{V}O_2$ ($\bar{x} \pm SE$) of albacore no. 11 as a function of PO_2 during runs 4, 5, and 6. The mean water temperature and fish swimming velocity during each run are: run 4 (14.4°C, 0.77 L/s), run 5 (14.9°C, 0.86 L/s), run 6 (18.0°C, 1.0 L/s). Run 4 began 2.7 h post capture, run 5 4.9 h post capture and run 6 at 5.8 h post capture. Note that the ordinal scales in A and B are different.

Although it was obtained for only 1 fish, the finding that albacore metabolism increases dramatically at 18°C, supports previous results (Graham and Dickson 1981; Graham and Laurs 1982) showing that prolonged exposure to temperatures above 18°C adversely affects this species. Albacore usually swim in 9°–14°C water below the mixed layer (Laurs et al. 1977, 1980) but rush up into warm surface water to feed. Albacore swimming in 18°C water cannot shed metabolic heat and became increasingly hyperthermic (Graham and Dickson 1981), and whereas fish in the ocean can always exercise the behavioural option of returning to deeper, cooler water to shed excess heat, fish in the respirometer cannot do this.

The mean $\dot{V}O_2$ of fish no. 11 at 18°C and in hypoxia (50–99 mmHg), was reduced to about the same rate of fish no. 5 in cooler temperatures and

in normoxia (Fig. 2), suggesting that increased temperature and hypoxia may have forced fish no. 11 to become partially anaerobic. Albacore may naturally experience PO_2 's as low as 60% of air saturation (90 mmHg), but this usually happens in cooler (9°–12°C) water (Laurs and Lynn 1977; Cech et al. 1984). Although the thermally induced left-shift of the albacore O_2 dissociation curve should prove beneficial for O_2 uptake in warm hypoxic water, the large Q_{10} effect on its $\dot{V}O_2$ apparently outweighs this enhancement. Further studies that assess albacore responses to abrupt changes in temperature and O_2 , such as those encountered by migration through and along oceanic fronts (Laurs and Lynn 1977), are needed, to define how factors such as swimming speed (i.e. heat production and $\dot{V}O_2$), haemoglobin- O_2 affinity, and behaviour may be integrated in metabolic responses to variable ambient conditions.

Acknowledgements. This work was supported by NSF DCB 84-16852 and DMB 85-00261. We thank the captain and the crew of the R.V. *David Starr Jordan* for assistance and support of this research.

References

- Breisch EA, White FC, Jones MH, Laurs RM (1983) Ultrastructural morphometry of the myocardium of *Thunnus alalunga*. *Cell Tissue Res* 233: 427–438
- Brett JR, Glass NR (1973) Metabolic rate and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J Fish Res Board Can* 30: 379–387
- Brill RW (1987) On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. *Fish Bull* 85: 25–35
- Cech JJ Jr, Laurs RM, Graham JB (1984) Temperature-induced changes in blood gas equilibria in the albacore, *Thunnus alalunga*, a warm-bodied tuna. *J Exp Biol* 199: 21–34
- Graham JB, Dickson KA (1981) Physiological thermoregulation in the albacore *Thunnus alalunga*. *Physiol Zool* 54: 470–486
- Graham JB, Laurs RM (1982) Metabolic rate of the albacore tuna *Thunnus alalunga*. *Mar Biol* 72: 1–6
- Jones DR, Brill RW, Mense DC (1986) The influence of blood gas properties on gas tensions and pH of ventral and dorsal aortic blood in free-swimming tuna, *Euthynnus affinis*. *J Exp Biol* 120: 201–213
- Lai NC, Graham JB, Lowell WR, Laurs RM (1987) Pericardial and vascular pressures and blood flow in the albacore tuna, *Thunnus alalunga*. *Exp Biol* 46: 187–192
- Laurs RM, Lynn RJ (1977) Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with Transition Zone waters. *Fish Bull* 75: 795–822
- Laurs RM, Yuen HSH, Johnson JR (1977) Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fish Bull* 75: 347–355

- Lauris RM, Ulevitch RJ, Morrison DC (1978) Estimates of blood volume in the albacore tuna. In: Sharp GD, Dizon AE (eds) The physiological ecology of tunas. Academic Press, New York, p 135
- Lauris RM, Dotson RC, Dizon A, Jemison A (1980) Observations on swimming depth and ocean temperature telemetered from free-swimming albacore. In: Wild A (ed) Proc 31st Tuna Conf, Inter-American Tropical Tuna Commission, La Jolla, California, pp 33-34
- Magnuson JJ (1978) Locomotion by scombrid fishes - hydrodynamics, morphology, and behavior. In: Hoar WS, Randall DJ (eds) Fish physiology, vol VII. Academic Press, New York, p 240
- Perry SF, Daxboeck C, Emmett B, Hochachka PW, Brill RW (1985a) Effects of temperature change on acid-base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. Comp Biochem Physiol 81A: 49-53
- Perry SF, Daxboeck C, Emmett B, Hochachka PW, Brill RW (1985b) Effects of exhausting exercise on acid-base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. Physiol Zool 58: 421-429
- Prange HD (1976) Energetics of swimming of a sea turtle. J Exp Biol 64: 1-12
- Tsukamoto K, Chiba K (1981) Oxygen consumption of yellowtail *Seriola quinqueradiata* in relation to swimming speed. Bull Jpn Soc Sci Fish 47: 673
- Webb PW (1971) The swimming energetics of trout II. Oxygen consumption and swimming efficiency. J Exp Biol 55: 521-540
- White FC, Kelly R, Kemper S, Schumacker PT, Gallagher KR, Lauris RM (1988) Organ blood flow haemodynamics and metabolism of the albacore tuna *Thunnus alalunga* (Bonnaterre). Exp Biol 47: 161-169

Received May 13, 1987/Accepted September 13, 1988
