Undersea Biomedical Research, Vol. 4, No. 3, September 1977

Hana Kai II: a 17-day dry saturation dive at 18.6 ATA.
V. Maximal oxygen uptake

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Dressendorfer, R. H., S. K. Hong, J. F. Morlock, J. Pegg, B. Respicio, R. M. Smith, and C. Yelverton. 1977. Hana Kai II: a 17-day dry saturation dive at 18.6 ATA. V. Maximal oxygen uptake. Undersea Biomed. Res. 4(3): 283–296.—Cardiorespiratory responses of four men to submaximal and maximal cycling exercise were observed during 17 days at 18.6 ATA. Inspired gas at pressure consisted of hyperoxic (P_{O_2} = 232 mmHg) and normoxic (P_{O_2} = 159 mmHg) helium mixtures with relative gas densities of 3.8 and 2.8, respectively. The average of pre- and postdive $\dot{V}_{O_2max}$ (1 ATA air), which were not significantly different, was 3.10 liters • min^{-1}. During 5 min of submaximal exercise at 50% of $\dot{V}_{O_2max}$, no significant difference in work rate, $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, $\dot{V}_E$, respiratory rate, heart rate (HR), stroke volume, blood pressures, or rectal temperature was noted at 18.6 ATA compared to 1 ATA with either gas mixture. Submaximal HR tended to decrease by 5 to 10 beats • min^{-1} at pressure, and in hyperoxia the $\dot{V}_{O_2}$/HR ratio was significantly higher. Maximal exercise was performed to exhaustion at work rates requiring about 120% of $\dot{V}_{O_2max}$. Significant increases in $\dot{V}_{O_2max}$ of 0.10 liter • min^{-1} (3%) and in endurance time of 2 min (48%) were found during hyperoxic gas breathing, whereas normoxic values at 18.6 ATA were similar to those at 1 ATA. Significant reductions in maximal HR of 8 beats • min^{-1} (4%) were observed with both gas mixtures at pressure, and $\dot{V}_E$ was significantly decreased by 36 liters • min^{-1} (26%) in hyperoxia and 29 liters • min^{-1} (21%) in normoxia. No change was found in the calculated cardiac output. Maximal voluntary ventilation, which was measured only for the hyperoxic gas, fell significantly by 80 liters • min^{-1} (40%). Results indicate that aerobic power and endurance performance were affected by oxygen pressure. Normoxic work capacity, however, was not decreased at 18.6 ATA, despite marked reductions in HR and $\dot{V}_E$.

hyperoxia	$\dot{V}_{O_2max}$
normoxia	MVV
exercise	cardiac output

Submaximal exercise tests conducted during simulated heliox dives of 500 to 1640 fsw have shown that metabolic and cardiorespiratory functions may become altered at pressure (Salzano, Rausch, and Saltzman 1970; Bradley, Anthonisen, Vorosmarti, and Linaweaver 1971;

Schaefer, Carey, and Dougherty 1971; Broussolle, Chouteau, Hyacinthe, LePechon, Burnet, Battesti, Cresson, and Imbert 1972; Flynn, Saltzman, and Summitt 1972; Strauss, Wright, Peterson, Lever, and Lambertsen 1972; Moore, Morlock, Lally, and Hong 1976). Maximal oxygen uptake ($\dot{V}_{O_2max}$) has not, however, been obtained in hyperbaric environments beyond 165 fsw (see, for example, Fagraeus 1974a) and there is only one report of maximal work performance at raised helium–oxygen pressure (Fagraeus 1974b). While $\dot{V}_{O_2max}$ can be predicted using submaximal oxygen uptake and heart rate, accuracy of the indirect method is considered no better than ± 10% (Andersen 1973). In addition, the $\dot{V}_{O_2max}$ of a diver may be limited by his ventilatory capacity before cardiac or metabolic limits are reached. Thus, our purpose was to make direct determinations of $\dot{V}_{O_2max}$ before, during, and after a prolonged saturation dive to 18.6 ATA in which hyperoxic helium was breathed. Since previous investigations have shown that hyperoxic gas mixtures increase $\dot{V}_{O_2max}$ and endurance performance (Fagraeus 1974b; Linnarsson, Karlsson, Fagraeus, and Saltin 1974; Ekblom, Huot, Stein, and Thorstensson 1975), a normoxic helium mixture was also administered to study effects of oxygen pressure on aerobic work capacity at 18.6 ATA. Overall objectives, design, and scope of the present dive are described in a preceding paper (Hong, Smith, Webb, and Matsuda 1977).

METHODS AND PROCEDURES

Subjects

Four healthy men participated as the subject divers (Table 1). With the exception of *BR*, they had above-average physical fitness and engaged in vigorous recreational activity. Repeated determinations of treadmill and cycling $\dot{V}_{O_2max}$ made before the dive indicated that all subjects had reproducible responses to maximal work. They were experienced, knowledgeable, and judged to be highly motivated for performing exercise to exhaustion.

Testing conditions

All experiments were conducted in the hyperbaric facility, *Aegir*. Tests at sea level (1 ATA air) were performed on the second and third days of pre- and postdive control periods, which lasted three days each. Bottom time at 18.6 ATA (14,118 mmHg) was 17 days. The first exercise experiment at 18.6 ATA occurred after 48 h at that pressure. Four or more days elapsed between tests on a given diver.

Physical properties of the inspired gases are shown in Table 2. At 18.6 ATA the chamber gas was hyperoxic (P_{O_2} = 232 mmHg). For normoxic experiments at 18.6 ATA the diver was administered a prepared helium–oxygen mixture (P_{O_2} = 159 mmHg) from outside the chamber.

Measurement techniques

Coordination between inside and outside research teams and the timing of experimental events were facilitated by two-way voice communication and monitoring over closed-circuit television. Methods used at sea level were the same as at pressure except for the gas sampling procedure which is discussed below.

Upright cycling exercise was performed on a Monarch mechanically braked ergometer (Varberg, Sweden) which was modified with racing type handlebars, saddle, pedals, and toe

TABLE 1
Description of Divers Including Maximal Cardiorespiratory Values for Treadmill Running

Diver	Age, yr	Ht, cm	Wt, kg	Fat*, %	$\dot{V}_{O_2 max}$ l•min⁻¹	$\dot{V}_{O_2 max}$ ml/kg/min	HR, b•min⁻¹	$\dot{V}_E$, l•min⁻¹ BTPS	Recreational activity, Smoking habits
JD	29	183	81.5	15.4	3.99	49.0	181	172.0	Occasional Scuba Diving and Regular Jogging (Pipe Smoker)
JM	29	184	68.4	14.5	3.83	56.5	178	124.6	Regular Surfing and Cycling (Non-Smoker)
BR	32	170	67.5	23.1	2.56	37.9	190	132.0	Occasional Scuba Diving (Heavy Smoker)
RS	32	172	63.3	15.1	3.14	49.6	175	126.5	Regular Jogging (Smoker)
Mean	31	177	70.2	17.0	3.38	48.2	181	138.8	

*Underwater weighing technique after Brozek, Grande, Anderson, and Keys (1963).

TABLE 2
Physical Properties of the Inspired Gases

Condition	ATA	P_B, mmHg	P_{O_2}, mmHg	P_{CO_2}, mmHg	P_{N_2}, mmHg	P_{He}, mmHg	T_a, °C	Relative Humidity %	Relative Gas Density
Pre- and Postdive	1	760	155	2.7	590	0	25.7	44	1
Hyperoxic	18.6	14118	232	2.7	825	13033	31.1	75	3.8
Normoxic	18.6	14118	159	0	~0	13926	31.8	~100	2.8

clips. Saddle height was adjusted to comfort and then standardized for each diver. Pedaling frequency was maintained at 60 ± 2 rpm, with pacing provided by a metronome. Maximal work loads were individually prescribed to produce muscular exhaustion within 3 to 5 min during tests at 1 ATA. Five minutes of preliminary exercise at 50% of $\dot{V}_{O_2max}$ and a 2-to-3-min recovery period preceded maximal work.

Oxygen uptake ($\dot{V}_{O_2}$) and carbon dioxide output ($\dot{V}_{CO_2}$) were measured using the open-circuit Douglas bag method. Expired gas was collected with the respiratory equipment described by Daniels (1971). The breathing valve had highly velocity, low resistance characteristics and a relatively small (75 ml) dead space. Expired gas volume was measured in a Parkinson-Cowan type CD4 dry gasmeter fitted with a rotary potentiometer that provided a continuous recording of pulmonary ventilation ($\dot{V}_E$,ATPS). Respiratory frequency (f_R) was counted from this breath-by-breath record. At sea level, gas samples were taken directly from 200-liter meteorological balloons containing the mixed expired minute volume. At 18.6 ATA, gas samples were transferred to thoroughly flushed 3-liter anesthesia bags outside the chamber via needle valves.

Composition of the inspired and expired gases was analyzed on triplicate samples by one person using a gas chromatograph (Quintron Model R, Milwaukee, Wisconsin). The two closest values for oxygen and carbon dioxide concentrations were averaged and used to calculate $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$. Calibration of the gas chromatograph was accomplished with reference gases of known composition (Scholander analysis) that approximated respiratory gas samples.

In normoxic experiments heliox was administered from high pressure cylinders outside the chamber. The gas was bubbled through water in a large plastic bottle inside the chamber and then flowed into a 200-liter meteorological balloon that was kept two-thirds filled. Gas sampled from this balloon was identical in oxygen content to that prepared in the high pressure cylinders, which indicated that there were no leaks along the gas line. The subject breathed from the balloon with no noticeable change in inspiratory airways resistance compared to that when breathing hyperoxic chamber gas. The normoxic gas was breathed for about 2 min before starting submaximal exercise, and was then breathed continuously to the end of maximal exercise. During normoxic experiments the chamber was vented to maintain pressure at 18.6 ATA.

Submaximal cardiorespiratory responses were observed during *minute 5*. Beginning with *minute 3* of maximal exercise, expired gas was collected minute-by-minute until the subject became exhausted and, despite encouragement, could no longer keep pace with the metronome. At that point, the subject was given a 10-s countdown, which ended exercise and gas collection. Endurance time (ET), therefore, represents the duration a subject's maximal work rate was voluntarily maintained. The average power output ($\dot{W}$) on the ergometer was calculated from continuous observations of the load setting and pedal frequency.

Since only $\dot{V}_E$ was measured, $\dot{V}_{O_2}$STPD and $\dot{V}_{CO_2}$STPD were calculated assuming that inert gas exchange (i.e., N_2 and He) was zero. This assumption seems valid since testing was done after two days at pressure and subjects were presumably saturated. Corrections were made for the measured concentration of carbon dioxide in the inspired gas. Values presented for $\dot{V}_E$BTPS and f_R were obtained over the last full minute of exercise; $\dot{V}_{O_2max}$ was defined as the highest $\dot{V}_{O_2}$ observed for a given condition. The standard error of measurement for repeated $\dot{V}_{O_2max}$ determinations in this Laboratory is on the order of $\pm$ 2%. For example, *subject JM* had a cycling $\dot{V}_{O_2max}$ of 3.71 $\pm$ 0.02 liters • min^{-1} (mean $\pm$ SD) in 16 previous tests.

Heart rate (HR) was determined from the continuously monitored electrocardiogram during *minute 5* of submaximal exercise and at the end of maximal work. Stroke volume (SV) was estimated using the noninvasive impedance method developed and described in detail by Kubicek, Kottke, Ramos, Patterson, Witsoe, Labree, Remole, Layman, Schoening, and Garamella (1974). Impedance SV was measured within the first 10 heart beats of recovery, and represents the average of 3 to 5 consecutive beats. During this immediate recovery period HR did not change significantly. Cardiac output ($\dot{Q}$) was calculated as the product of HR and SV. According to data previously reported (Gilbert, Auchincloss, and Baule 1967; Davies, DiPramprero, and Cerretelli 1972) $\dot{Q}$ decreases less than 3% within the first 10 s after heavy exercise. The accuracy of $\dot{Q}$ values in exercising subjects measured by impedance was recently validated against the indicator dilution method (Denniston, Maher, Reeves, Cruz, Cymerman, and Grover 1976).

Blood pressures (BP) were measured by sphygmomanometry during *minute 5* of submaximal exercise. Because of vigorous use of the arms and background noise, it was not possible to obtain reliable BP readings in maximal work. Rectal temperature (T_{re}) was measured during the last 30 s of exercise using a Yellow Springs telethermometer with the thermistor probe inserted 15 cm beyond the external anal sphincter. Maximal voluntary ventilation (MVV) was measured 10 min after maximal exercise while the subject was still in the exercise position and inspiring ambient chamber gas. A 15-s test allowing free choice of breathing frequency and depth was used and the higher value of two trials recorded. Determinations of MVV were not made when subjects inspired the normoxic gas mixture at 18.6 ATA.

Anaerobic work capacity was estimated one week before and after the dive using a 1-min cycling test (Szogy and Cherebetiu 1974). Load settings on the Monarch ergometer were approximately 0.5 kilopond (kp) higher than those used for tests of aerobic work capacity. After a short practice period, subjects were instructed to make the highest possible number of revolutions in 1 min. Despite physical efforts which were clearly maximal, no subject achieved more than 100 revolutions. Anaerobic capacity was defined as oxygen deficit during the 1-min test, which was calculated by converting total work output (kpm) to its metabolic equivalent (i.e., oxygen cost corrected for mechanical efficiency) and subtracting the observed $\dot{V}_{O_2}$ during work.[1]

Statistical significance of a difference between mean values at 18.6 ATA compared to the 1 ATA control was analyzed on intraindividual differences by using paired *t* tests and the conventional level of significance ($P < 0.05$).

RESULTS

Pre- and postdive tests

Results of aerobic and anaerobic work capacity tests before and after the dive are shown in Fig. 1. Predive tests were not conducted on *subject BR;* however, $\dot{V}_{O_2max}$ from a previous study was similar to his postdive $\dot{V}_{O_2max}$. In the three other subjects, postdive $\dot{V}_{O_2max}$ was within $\pm$ 0.05 liter • min^{-1} of their predive values, which was within the range of accuracy for the measurement. Similarly, HR, $\dot{Q}$, and $\dot{V}_E$ during maximal tests after the dive showed no remarkable changes from predive values, although endurance time was slightly reduced in *subjects JD* and *JM* and increased in *subject RS*. All three subjects *(JD, JM, RS)* remarked that in postdive tests leg weakness seemed to be the major subjective factor limiting their endurance, whereas in predive tests the onset of leg fatigue and breathlessness occurred together. Results of anaerobic work capacity (oxygen deficit) tests paralleled the observed changes in endurance for *subjects JD* and *JM* (Fig. 1), suggesting they may indeed have lost some leg strength during the dive. Despite this possibility, however, it was clear that cardiorespiratory responses to maximal aerobic work were unchanged after the dive. We therefore felt justified in using the postdive responses of *subject BR* for a control; consequently, pre- and postdive results were averaged for the other three subjects to represent their 1 ATA control.

Submaximal exercise

Results of submaximal exercise experiments are shown in Table 3. Relative work loads averaged about 50% of $\dot{V}_{O_2max}$. There were no significant differences in $\dot{W}$ or $\dot{V}_{O_2}$ with either gas mixture at 18.6 ATA. Likewise, there were no statistically significant differences in the

[1]One liter of oxygen was assumed to be equivalent to 2150 kilpond-meters. Calculated mechanical efficiency during steady-state submaximal work was 19.5%.

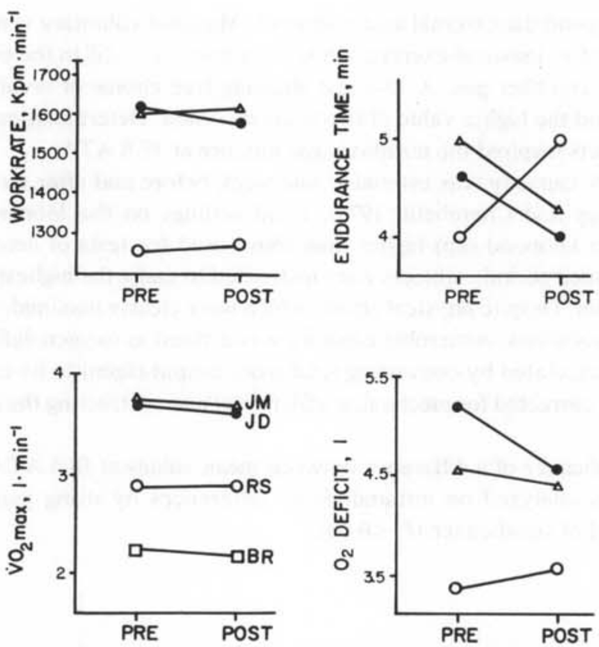

Fig. 1. Results of aerobic ($\dot{V}_{O_2max}$, work rate, and endurance time) and anaerobic (oxygen deficit) work capacity cycling tests conducted 1–2 days before (pre) and after (post) saturation diving to 18.6 ATA. Predive $\dot{V}_{O_2max}$ for *subject BR* was obtained 2 years before the present study.

observed cardiorespiratory responses. However, notable reductions in HR (8%), $\dot{V}_E$ (9%), and R (8%) occurred at 18.6 ATA with hyperoxic helium breathing, and the derived ratio, $\dot{V}_{O_2}$/HR, was significantly higher. These responses returned toward 1 ATA values when normoxic helium was breathed. Blood pressures and T_{re} at 18.6 ATA were unchanged from control values. There were no reports of dyspnea during submaximal exercise.

Maximal exercise

Responses to maximal exercise at 1 ATA and at 18.6 ATA while breathing hyperoxic or normoxic helium are shown in Table 4 and Fig. 2. The average $\dot{W}$ was 1390 kpm · min^{-1} and, as estimated from the mechanical efficiency of steady-state submaximal exercise, had an oxygen cost of approximately 3.7 liters · min^{-1} or about 120% of $\dot{V}_{O_2max}$ for all conditions. At 1 ATA, $\dot{V}_{O_2max}$ and endurance time (ET) were 3.10 liters · min^{-1} and 4.19 min, respectively.

During hyperoxic helium breathing, $\dot{V}_{O_2max}$ was 3.20 liters · min^{-1} or 0.10 liter · min^{-1} (3%) greater than for 1 ATA. This small increase was statistically significant. In hyperoxia there was a significant increase in endurance of 2.0 min (48%) and, with the exception of *subject JD*, the work was reportedly less difficult. Maximal $\dot{V}_{CO_2}$ decreased 0.21 liter · min^{-1} (6%), resulting in a significantly lower R during hyperoxic helium breathing.

When normoxic helium was breathed, $\dot{V}_{O_2max}$ was equal to the 1 ATA air value. In two experiments the normoxic gas supply ran out before the subject was exhausted (Table 4). Nevertheless, it was clear that compared to 1 ATA, endurance was not reduced during maximal exercise at 18.6 ATA in normoxia.

TABLE 3

Metabolic and Cardiorespiratory Responses to Submaximal Cycling Exercise in Divers Breathing Air at 1 ATA, Hyperoxic Helium at 18.6 ATA, and Normoxic Helium at 18.6 ATA

Diver	P_B, ATA	P_{O_2}, mmHg	$\dot{W}$, kpm•min⁻¹	$\dot{V}_{O_2max}$, %	$\dot{V}_{O_2}$, l•min⁻¹	$\dot{V}_{CO_2}$, l•min⁻¹	R	HR, b•min⁻¹	SV, ml	$\dot{Q}$, l•min⁻¹	BP, mmHg	$\dot{V}_E$, l•min⁻¹ BTPS	f_R, br•min⁻¹	T_{re}, °C
	1	155	740	53	1.93	1.71	.88	133	126	16.5	178/84	51.4	19	37.4
JD	18.6	225	722	51	1.92	1.58	.82	110	146	16.1	160/80	51.3	26	37.2
	18.6	158	684	46	1.68	1.61	.96	115	135	15.5	160/85	48.3	23	37.1
	1	155	726	48	1.77	1.65	.93	126	136	17.2	167/79	48.9	18	37.6
JM	18.6	226	720	46	1.76	1.41	.80	120	140	16.8	160/75	43.8	16	37.3
	18.6	161	720	50	1.86	1.68	.90	127	—	—	170/80	45.7	15	37.4
	1	155	454	53	1.15	.97	.84	142	73	10.4	155/100	32.7	20	37.4
BR	18.6	219	465	56	1.26	1.04	.83	142	77	10.9	170/85	32.1	17	37.2
	18.6	158	454	54	1.19	1.18	.99	149	70	10.5	150/95	34.9	19	37.5
	1	155	544	52	1.51	1.28	.85	121	94	11.4	165/90	41.0	19	37.2
RS	18.6	260	513	55	1.64	1.32	.80	109	100	10.9	168/80	31.4	15	37.4
	18.6	161	522	50	1.41	1.38	.98	109	111	12.1	158/90	41.2	16	37.2
	1	155	616	51	1.59	1.40	.88	130	107	13.9	166/86	43.5	19	37.4
Mean	18.6	232	605	51	1.64	1.34	.81	120	116	13.7	164/80	39.6	18	37.3
	18.6	159	595	50	1.54	1.46	.95	125	—	—	160/88	42.5	18	37.3

$n = 4$.

TABLE 4
Metabolic and Cardiorespiratory Responses to Maximal Cycling Exercise in Divers Breathing Air at 1 ATA, Hyperoxic Helium at 18.6 ATA, and Normoxic Helium at 18.6 ATA

Diver	P_B, ATA	P_{O_2}, mmHg	$\dot{W}$, kpm • min⁻¹	ET, min	$\dot{V}_{O_2max}$, l • min⁻¹	$\dot{V}_{CO_2}$, l • min⁻¹	R	HR, b • min⁻¹	SV, ml	$\dot{Q}$, l • min⁻¹	$\dot{V}_E$, l • min⁻¹, BTPS	f_R, br • min⁻¹	T_{re}, °C
	1	155	1600	4.31	3.64	4.33	1.19	182	132	24.0	180.0	59	37.8
JD	18.6	225	1668	4.92	3.75	4.21	1.12	166	132	21.9	124.6	39	37.5
	18.6	158	1566	4.62	3.64	4.18	1.15	170	136	23.1	134.9	38	37.1
	1	155	1618	4.62	3.69	4.31	1.17	179	136	24.3	131.2	47	38.1
JM	18.6	226	1539	7.00	3.86	4.13	1.07	175	142	24.8	91.8	41	37.9
	18.6	161	1683	4.42†	3.72	3.84	1.03	173	—	—	95.2	37	37.4
	1	155	1107	3.33	2.19	2.61	1.19	186	72	13.4	97.2	42	37.6
BR	18.6	219	1111	4.95	2.24	2.49	1.11	180	75	13.5	92.1	39	37.4
	18.6	158	1062	4.00	2.20	2.74	1.25	184	72	13.2	99.8	46	37.6
	1	155	1264	4.50	2.88	3.49	1.21	185	94	17.4	139.8	39	37.5
RS	18.6	260	1263	8.00	2.96	3.04	1.03	178	101	18.0	95.7	29	37.6
	18.6	161	1202	6.50†	2.84	3.09	1.09	173	110	19.1	102.4	28	37.2
Mean	1	155	1397	4.19	3.10	3.68	1.19	183	108	19.8	137.1	47	37.8
	18.6	232	1395	6.22*	3.20*	3.47	1.08*	175*	112	19.6	101.0*	37*	37.6
	18.6	159	1378	4.88	3.10	3.46	1.13	175*	—	—	108.1*	37	37.3

*Significantly different ($P < 0.05$) from 1 ATA; ET = endurance time; † = subjective evaluation by diver; normoxic gas supply ran out 0.5 min before this projected endurance time; $n = 4$.

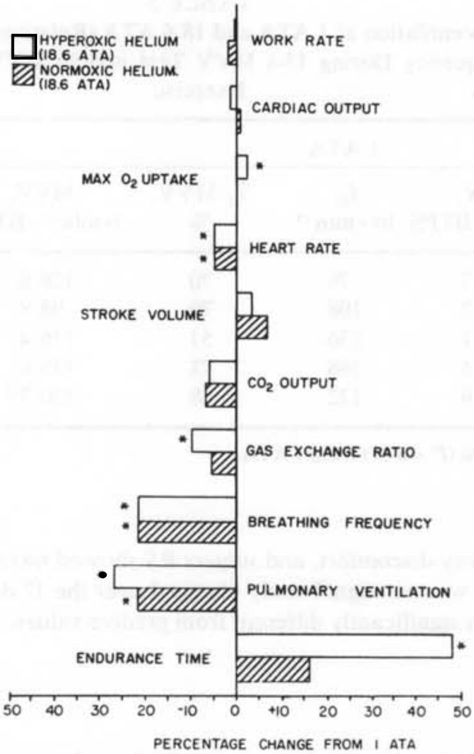

Fig. 2. Percentage changes in 1 ATA work performance and cardiorespiratory function of 4 divers during maximal effort cycling tests at 18.6 ATA while breathing hyperoxic or normoxic helium. Statistically significant changes are indicated by an asterisk.

Maximal HR at 18.6 ATA was significantly decreased from 183 beats $\cdot min^{-1}$ at 1 ATA to 175 beats $\cdot min^{-1}$. This average reduction of 8 beats $\cdot min^{-1}$ (4%) was similar to that observed during submaximal exercise and was unrelated to oxygen pressure. There were no consistent changes in SV or $\dot{Q}$ at pressure. The calculated arterio-venous oxygen difference was 158 ml $\cdot liter^{-1}$ at 1 ATA and 164 ml $\cdot liter^{-1}$ during hyperoxic helium breathing.

Expired minute volume decreased significantly (26%) from the 1 ATA value of 137.1 liter $\cdot min^{-1}$ to 101.0 liter $\cdot min^{-1}$ in hyperoxic helium. In normoxic helium, $\dot{V}_E$ was 7.1 liter $\cdot min^{-1}$ higher than for hyperoxia, but still significantly lower (21%) than that at 1 ATA. The reductions in $\dot{V}_E$ were caused primarily by lower respiratory frequency at pressure, since tidal volume was not significantly different.

Hyperbaric helium had no significant effect on T_{re} (though lower values were noted at 18.6 ATA) despite the higher ambient temperature and humidity and longer duration of maximal exercise. In the normoxic condition at 18.6 ATA, there was surprisingly little increase in T_{re} from submaximal to maximal exercise (Table 4).

Maximal voluntary ventilation decreased 80 liter $\cdot min^{-1}$ (40%) at pressure (Table 5). Reductions in both rate and depth of breathing were responsible for the lowered MVV. The ratio of $\dot{V}_E$ during maximal exercise to MVV increased on the average from 68% at 1 ATA to 85% at 18.6 ATA. One subject (*JD*) nearly equalled his MVV during maximal exercise (Table 5) and reported considerable dyspnea. Another subject (*JM*), however, utilized 93% of MVV without

TABLE 5

Maximal Voluntary Ventilation at 1 ATA and 18.6 ATA (Relative Gas Density = 3.8) Including Respiratory Frequency During 15-s MVV Test and % MVV Utilized During Maximal Exercise

	1 ATA			18.6 ATA		
Diver	MVV, $l \cdot min^{-1}$, BTPS	f_R, $br \cdot min^{-1}$	$\dot{V}_E$/MVV, %	MVV, $l \cdot min^{-1}$, BTPS	f_R, $br \cdot min^{-1}$	$\dot{V}_E$/MVV, %
JD	255.3	76	70	126.6	56	98
JM	165.2	108	79	98.8	92	93
BR	192.1	136	51	116.4	104	79
RS	191.4	168	73	139.4	96	69
Mean	201.0	122	68	120.3*	87*	85

*Significantly different ($P < 0.05$) from 1 ATA.

experiencing respiratory discomfort, and *subject RS* showed no change in this ratio. Maximal voluntary ventilation was not significantly changed over the 17 days spent at 18.6 ATA, nor were postdive MVV's significantly different from predive values.

DISCUSSION

Physical activity during the dive was generally less than each subject's habitual level. Despite confinement, however, the divers were not inactive. In addition to performing the two scheduled submaximal and maximal work experiments, they did voluntary ergometer exercise, which was strenuous on some days, and also participated in a 30-min submaximal exercise test. On the other hand, they did no exercise for seven days during decompression. Since postdive $\dot{V}_{O_2max}$ was not significantly different from predive values (Fig. 1), it can be assumed that their aerobic capacity for brief bouts of maximal work was unaffected by any physical deconditioning.

The ergometric relationship between work rate and oxygen uptake during submaximal exercise was not significantly changed by either total pressure or oxygen pressure (Table 3). This observation agrees with similar findings by others (Kaijser 1970; Lally, Moore, and Hong 1971; Broussolle et al. 1972; Camporesi, Salzano, Fortune, Saltzman, Fagraeus, and Argeles 1975; Moore et al. 1976), whereas increases in $\dot{V}_{O_2}$ ranging from 10 to 21% for a given work load at pressure have been reported (Salzano et al. 1970; Taunton, Banister, Patrick, Oforsagd, and Duncan 1970; Bradley et al. 1971; Schaefer et al. 1971; Fagraeus 1974a). Salzano et al. (1970) found $\dot{V}_{O_2}$ increased about 0.35 liter $\cdot min^{-1}$ during submaximal exercise at 31.3 ATA, which they attributed to a greater work of breathing. In the present study, values for $\dot{W}$, $\dot{V}_E$, P_{O_2}, and relative gas density during submaximal exercise in the hyperoxic condition were similar to those of Salzano et al. (1970), but only an 0.05 liter $\cdot min^{-1}$ increase in $\dot{V}_{O_2}$ was observed over 1 ATA. Also, no difference in $\dot{V}_{O_2}$ was found during hyperbaric normoxia. Thus, any increased work of breathing dense gas in the 18.6 ATA environment had little effect on $\dot{V}_{O_2}$ during submaximal exercise. It is assumed, therefore, that large elevations in exercise $\dot{V}_{O_2}$ found in earlier heliox dives were primarily caused by factors other than respiratory work. One such possible explanation might be cold stress. For example, Moore and his associates (1976) were able to reduce the elevated $\dot{V}_{O_2}$ during submaximal exercise at 16.1 ATA to the 1 ATA value by increasing ambient temperature.

An increase of 0.10 liter • min^{-1} in $\dot{V}_{O_2max}$, although within the accuracy of our method, was found at 18.6 ATA during helium breathing when P_{O_2} was 232 mmHg. Decreasing P_{O_2} to 159 mmHg at 18.6 ATA reduced $\dot{V}_{O_2}$max to 1 ATA levels (Table 4 and Fig. 2). Thus total pressure did not affect $\dot{V}_{O_2max}$, whereas oxygen pressure had a slight potentiating effect. It is unfortunate that $\dot{V}_{O_2max}$ while breathing the hyperoxic gas mixture was not determined at 1 ATA because others have shown that moderate hyperoxia increases aerobic work capacity (Ekblom et al. 1975). In such a case, we might have observed a reduction in hyperoxic $\dot{V}_{O_2max}$ at 18.6 ATA caused by a ventilatory limitation (Fagraeus 1974a).

Hyperoxia also produced a significantly longer endurance time. In terms of total work output, the subjects performed 2823 kpm more work during maximal exercise at 18.6 ATA in hyperoxia than at 1 ATA, and 1952 kpm more work than with normoxia at 18.6 ATA. Clearly, only a small fraction of the energy required for the additional work can be explained by an 0.10 liter • min^{-1} increase in $\dot{V}_{O_2max}$. Thus, the additional work was mostly anaerobic, or was supported, at least in part, by oxygen stores.

The present findings concerning increased endurance time are in disagreement with Fagraeus (1974b), who found a similar 3% increase in $\dot{V}_{O_2max}$ during air breathing at 6.0 ATA but no change in endurance time. However, the work loads used by Fagraeus had an oxygen cost of 140% of $\dot{V}_{O_2max}$ compared to a 120% cost in the present study. Differences in the anaerobic work component may prevent a valid comparison because, as shown by Fagraeus (1974a) and Linnarsson et al. (1974), the extent of blood and muscle lactate accumulation may be a major determinant of endurance time. Since in the present study $\dot{V}_{O_2}$ was a greater percentage of total oxygen cost, less anaerobic glycolysis would be required. The longer endurance time found at 18.6 ATA during hyperoxia might be more related to a possible reduction in lactate production than to the observed increase in $\dot{V}_{O_2max}$.

The finding that aerobic work capacity was unchanged during normoxic conditions at 18.6 ATA compared to 1 ATA agrees with observations of submaximal work made by Strauss et al. (1972), who found that two divers were able to perform the same progressive exercise regimen (up to 80% of maximal $\dot{W}$) at 37 ATA while breathing normoxic helium as they could during air breathing at 1 ATA. The present results are particularly interesting because normoxic $\dot{V}_{O_2max}$ at pressure was unchanged despite significant reductions in HR and $\dot{V}_E$. Other adjustments in oxygen transport, such as increased stroke volume and pulmonary oxygen extraction, must have occurred to compensate for the lower HR and $\dot{V}_E$.

Reductions in resting and exercise HR at pressure are well documented (Kaijser 1970; Salzano et al. 1970; Taunton et al. 1970; Bradley et al. 1971; Lally et al. 1971; Schaefer et al. 1971; Flynn, Berghage, and Coil 1972; Fagraeus 1974a; Moore et al. 1976). Submaximal and maximal HR were reduced to about the same extent at 18.6 ATA and were largely unaffected by oxygen pressure. This finding suggests that HR as a function of $\dot{V}_{O_2}$ remains a linear relationship in the hyperbaric environment throughout the range of exercise tolerance (Salzano et al. 1970). Hyperbaric bradycardia is thought to result from separate effects of oxygen and nitrogen pressures, gas density, and total pressure (Fagraeus 1974a; Flynn, Berghage, and Coil 1972). Since maximal HR was the same for both conditions at 18.6 ATA, oxygen pressure may be discounted as a major factor. Furthermore, the reduction in gas density and elimination of nitrogen (Table 2) seemed to have little effect. Thus, the 8 beats • min^{-1} reduction in maximal HR at 18.6 ATA probably was caused either by helium or by pressure per se. The mechanism for a relative bradycardia at pressure remains unknown, although recent experiments by Hogan and Örnhagen (personal communication) on isolated rat heart indicate that pressure per se can suppress the depolarization rate of SA nodal cells. More detailed discussions on hyperbaric bradycardia are presented in a companion paper by Smith, Hong, Dressendorfer, Dwyer, Hayashi, and Yelverton (1977).

Lack of significant changes in exercise $\dot{Q}$ agrees with previous studies (Kaijser 1970; Camporesi et al. 1975) and implies that SV must increase to offset the relative bradycardia; however, the observed changes in SV were small and not statistically significant. Systolic and diastolic blood pressures observed during submaximal exercise were similar under all conditions, and are in agreement with Fagraeus, Haggendal, and Linnarsson 1973 (compare Fagraeus 1974a); these authors found no change in mean arterial pressure during submaximal exercise at 6 ATA in air.

Expired minute volume during submaximal work showed only a slight decrease at 18.6 ATA, which supports results of previous studies (Salzano et al. 1970; Bradley et al. 1971; Schaefer et al. 1971; Fagraeus 1974a; Moore et al. 1976) and suggests that relative gas densities up to 3.8 create negligible airways resistance at ventilatory flow rates of 40 liters $\cdot$min^{-1} with low-resistance breathing devices. The unchanged respiratory frequency found in this study would support this conclusion. During maximal exercise, however, $\dot{V}_E$ was significantly lower at pressure. The apparent discrepancy is not surprising, since during dense gas breathing airways resistance increases as an exponential function of flow rate (Maio and Farhi 1967). The marked resistance to breathing dense gases at high flow rates was demonstrated by Strauss et al. (1972) and is also reflected by our observed 40% reduction in MVV, which was similar to that predicted by Maio and Farhi (1967) and by Lanphier (1969). A probable explanation for the 7% higher $\dot{V}_E$ in normoxic versus hyperoxic gas breathing is the lower gas density, although, as suggested above, anaerobiosis and consequently the chemical drive to ventilation may have been reduced by breathing hyperoxic gas.

Although alveolar hypoventilation was not verified, the significant reduction in R during maximal exercise with hyperoxic helium suggests the presence of carbon dioxide retention, and yet only one diver (*JD*) felt his work capacity was limited by an inability to increase ventilation. In his case, peak $\dot{V}_E$ reached 98% of MVV (Table 5). On the other hand, diver *JM* utilized 93% of his MVV during maximal exercise without experiencing a respiratory limitation. Demedts and Anthonisen (1973) showed that when maximal exercise ventilation is limited by external airway resistance at 1 ATA, peak $\dot{V}_E$ and MVV are lowered proportionately, i.e., the $\dot{V}_E$/MVV ratio remains about 70–75%. Their findings do not seem to apply to dense gas breathing without external airway resistance. Broussolle et al. (1972) reasoned that subjects who utilize a low percentage of their MVV during work at sea level would be less affected by ventilatory restrictions at pressure, and would perhaps be good candidates for deep dives. Using their criterion, however, we could not have predicted the respiratory difficulty encountered by diver *JD*.

Figure 2 summarizes the changes in percent of maximal cardiorespiratory function and work performance observed at 18.6 ATA. The results clearly show that aerobic power and work capacity were not reduced at pressure despite significant reductions in HR, $\dot{V}_E$, and MVV. Indeed, the hyperoxia which is often associated with deep dives served to improve physical endurance. The observed increase of 3% in $\dot{V}_{O_2max}$ with hyperoxic gas breathing at 18.6 ATA was small in comparison to other reports of maximal exercise during hyperoxia (Fagraeus, Hesser, and Linnarsson 1974; Ekblom et al. 1975). It seems possible, therefore, that without the decrease in maximal pulmonary ventilation at 18.6 ATA, which can be attributed to increased gas density, the potential for improving $\dot{V}_{O_2max}$ might have been greater.

We wish to express our gratitude to the subjects for their cooperation and high degree of motivation. We are also indebted to Gosta Fahlman, Operations Director, and Edwin Hayashi, master diver on board *Aegir*, for their expert technical advice and assistance. This research was supported by Office of Naval Research contracts N00014–75–C–0404 and N00014–67–A–0387–0016, with funds provided by the Naval Medical Research and Development Command, NOAA Sea Grant 04–3–158–29, and State of Hawaii Marine Affairs Coordinator's Office Task Order MT–001.—*Manuscript received for publication May 1976; revision received August 1976.*

Dressendorfer, R. H., S. K. Hong, J. F. Morlock, J. Pegg, B. Respicio, R. M. Smith, and C. Yelverton. 1977. Hana Kai II: Plongée fictive à saturation, 17 jours à 18,6 ATA. V. Consommation maximale d'oxygène. Undersea Biomed. Res. 4(3): 283–296.—Les réponses cardiorespiratoires à un exercise sous-maximal et maximal à la bicyclette erogmétrique ont été observées chez 4 sujets pendant 17 jours à 18,6 ATA. En compression, les sujets ont respiré des mélanges hyperoxique (P_{O_2} = 232 mmHg) et normoxique (P_{O_2} = 159 mmHg) d'hélium–oxygène, a des densités gazeuses relatives de 3,8 et 2,8, respectivement. Le moyen des valeurs pré-et post-plongée de la consommation maximale d'oxygène ($\dot{V}_{O_2max}$) (1 ATA air) était 3,10 l/min^{-1}. (Pas de différence significative entre les deux valeurs) Pendant 5 min d'exercise sous-maximal à 50% de $\dot{V}_{O_2max}$, aucun changement de la vitesse de travail, de $\dot{V}_{O_2}$, de $\dot{V}_{CO_2}$, de $\dot{V}_E$, de la fréquence respiratoire, de la fréquence cardiaque, du débit systolique, de la pression artérielle, ni de la température rectale n'a été observé à 18,6 ATA en les deux mélanges, par comparison aux valeurs établies à 1 ATA. La fréquence cardiaque sous-maximale a augmenté de 5 à 10 b/min^{-1} à la pression maximale, et le rapport $\dot{V}_{O_2}$: fréquence cardiaque était plus élevé. Le travail de l'exercise maximal à l'épuisement a requis environ 120%. du $\dot{V}_{O_2max}$. On a observé des augmentations significatives de $\dot{V}_{O_2max}$ (0,10 l/min^{-1} ou 3%) et de temps d'endurance (2 min ou 48%) au cours de la respiration de mélanges hyperoxiques, tandis que les valeurs à 18,6 ATA en normoxie ressemblaient à celles observées à 1 ATA. On a constaté des baisses significatives de fréquence cardiaque maximale (8 b/min^{-1} ou 4% en hyperoxie comme en normoxie, à la pression maximale), et de $\dot{V}_E$ (36 l/min^{-1} ou 26% en hyperoxie; 29 l/min^{-1} ou 21% en normoxie). Le débit cardiaque calculé n'a pas changé. La capacité respiratoire maximale, déterminée en hyperoxie seulement, a baissé significativement (80 l/min^{-1} ou 40%). La pression d'oxygène a donc influé sur la force aerobique et l'endurance. Cependant la capacité de travail en normoxie n'a pas baissé à 18,6 ATA, malgré des chutes importantes de fréquence cardiaque et de $\dot{V}_E$.

hyperoxie	$\dot{V}_{O_2max}$
normoxie	capacité respiratoire maximale (MVV)
exercise	débit cardiaque

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