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Effects of breathing-gas pressure on pulmonary function and work capacity during immersion

N. A. S. TAYLOR and J. B. MORRISON

Kinesiology, Division of Sciences, University of Otago, P.O. Box 56, Dunedin, New Zealand; and School of Kinesiology, Simon Fraser University, Burnaby, B.C. V5A 1S6, Canada

Taylor NAS, Morrison JB. Effects of breathing-gas pressure on pulmonary function and work capacity during immersion. Undersea Biomed Res 1990; 17(5):413–428.—Upright immersion induces respiratory mechanical changes that may impair pulmonary function during hyperbaric exercise. To evaluate this, 10 divers performed an incremental cycling protocol while immersed upright at 1.02 and 6.05 atmospheres absolute (atm abs). Air was supplied at each of two hydrostatic pressures: mouth pressure (P_m: to simulate a mouth-held demand regulator) and lung centroid pressure (P_{LC}). Subjects perceived air delivery at P_{LC} to be more comfortable at each level of exercise at both absolute pressures ($P < 0.05$). At 6.05 atm abs subjects perceived narcosis to be greater for P_m than for P_{LC} air delivery. Hypoventilation was encountered at 6.05 atm abs with P_{LC} air delivery and was further exacerbated when air was delivered at P_m ($P < 0.05$). It was concluded that hypoventilation and narcosis are reduced whereas respiratory comfort is increased when air is delivered at P_{LC}. This change is possibly due to improved pulmonary mechanics accompanying P_{LC} air supply pressure.

diving	hyperbaric
exercise	immersion
breathing pressure	lung centroid pressure
hypercapnia	dyspnea
static lung loading	breathing apparatus
ventilation	negative pressure breathing

Normobaric physical power is generally limited by cardiovascular rather than respiratory mechanisms (1–3). It has been postulated that immersion without breathing pressure compensation may induce respiratory mechanical perturbations capable of reducing physical power (4–6). Such changes may result in ventilatory-dependent exercise intolerance, similar to that seen in patients with chronic obstructive pulmonary disease, and would be exacerbated under hyperbaric states.

Numerous research groups have investigated the effects of pressure on aerobic power, with divergent observations. During nonimmersion trials at depths from 1 to 6 atmospheres absolute (atm abs), Fagraeus et al. (7), Fagraeus (8), Anthonisen et al. (9), and Linnarsson and Fagraeus (10) failed to observe decrements in aerobic power. Dressendorfer et al. (11) found that maximal aerobic power during immersed exercise at 1 atm abs (head-out cycling) was reduced along with minute ventilation when compared with dry control data.

Several groups have investigated aerobic power of the immersed diver under hyperbaric states. Morrison (12) reported prone swimming subjects to experience respiratory difficulty, and although some subjects were unable to complete the exercise protocol, a consistent aerobic power decrement was not apparent.

Dwyer et al. (13) investigated upright, immersed divers at a pressure of 43.4 atm abs using a helium-oxygen breathing mixture. Unlike the above dry experiments at lower absolute pressures but approximately equivalent gas density, they found maximal aerobic power to be reduced. The authors concluded that factors other than gas density were responsible for the observed power decrement. Similarly, Spaur et al. (14) reported an inability of subjects to exercise at an oxygen uptake in excess of 1.92 liter $\cdot$ min^{-1} when breathing heliox and immersed upright at 49.5 atm abs. They attributed this to a density-dependent increase in airway resistance (R_{aw}).

Thalmann et al. (5) studied the influence of air supply pressure (using hydrostatic loading) on prone, immersed exercise at pressures from 1.45 to 6.76 atm abs. (Hydrostatic loading was obtained by changing the depth of the subject in the water, thereby altering body surface pressure relative to the ambient air supply pressure. A neutral position was achieved when the center of the body was in the same horizontal plane as the water surface on the dry side of a Morin-Lanphier barrier.) A lower maximal minute ventilation was observed when subjects were exposed to a negative breathing pressure. Maximal aerobic power increased with changes in absolute pressure when breathing air at a neutral hydrostatic load. However, only 1 subject ($n = 3$) was able to complete maximal exercise trials with a hydrostatic breathing load of -0.98 kPa at 6 atm abs. All subjects completed submaximal trials at loads of -1.98 and -0.98 kPa, although dyspneic sensations were greater and often severe.

When a diver is immersed upright and breathes air from a mouth-held demand regulator, the mean hydrostatic pressure acting on the thorax exceeds air delivery pressure. This is physically analogous to negative pressure breathing and is referred to as uncompensated breathing. Breathing pressure compensation involves elevating the air supply pressure to approximate this external thoracic pressure, the lung centroid pressure (P_{LC}) (15). P_{LC} is defined as the breathing pressure required to restore the immersed respiratory relaxation volume to its control value.

It has previously been demonstrated that upright immersion with uncompensated air delivery pressures elevates total respiratory static work (16–18), flow-resistive pulmonary work (16, 19, 20), and pulmonary and airway resistance (20–23). Work by Taylor et al. (18) has illustrated the capacity of hydrostatic breathing pressure compensation to return static respiratory mechanical attributes toward control status.

Both static breathing load and changes in gas density seem to influence physical power during immersed exercise with a raised absolute pressure. It is of interest to professional divers to know whether breathing pressure compensation may improve respiratory mechanics during immersed exercise and, in so doing, increase physical capacity. It was hypothesized that elastic and flow-resistive respiratory work increments attending uncompensated hydrostatic breathing pressures during upright, immersed exercise would magnify the density-dependent ventilatory limitations encountered at depth. Compensation of hydrostatic breathing pressure to match P_{LC} was envisaged as ameliorating this restraint, enabling increments in exercise minute ventilation and respiratory comfort under hyperbaric conditions.

METHODS

Subjects were required to perform fatiguing exercise at 1.02 and 6.05 atm abs while immersed upright and were supplied with air at each of two hydrostatic breathing pressures: mouth pressure (P_m) and (P_{LC}) (15).

Subjects

Ten males with diving experience were screened for normal lung function history and physical disorders that would contraindicate hyperbaric exposure. Subjects were nonsmokers and less than 35 yr of age, with a predicted maximal aerobic power greater than 40 ml · kg^{-1} · min^{-1} (24).

Apparatus

Experiments were performed in the wet chamber of a hypo-hyperbaric chamber complex able to simulate depths to 300 m with temperature and humidity control. Water temperature was regulated at 28.6 ± 0.9°C. Subjects exercised using a hydraulic cycle ergometer (crank radius = 0.17 m), with the legs extended forward and downward producing a semireclining lower body position, while the back remained vertical.

A neckseal diving helmet (Kirby Morgan super-light, U.S. Divers) was modified to facilitate: a) the attachment to a movable demand regulator, used to produce breathing pressure variations (hydrostatic loads); b) equilibration of breathing pressure and facial surface pressure; c) measurement of the pressure differential between the mouth and demand regulator; and d) collection of end-tidal gas samples (Fig. 1). These modifications resulted in an elevation of the respiratory apparatus dead space, which at a minimum would be 750 ml, and included the oronasal mask, the low resistance tubing leading to the demand regulator, and possibly some portion of the helmet air space outside the oronasal mask (Fig. 1).

Air was provided via a Conshelf 30 demand regulator (U.S. Divers). Morrison et al. (25) found this regulator to fulfill tolerance and comfort requirements at depths to 50 m and at ventilations to 60 liter · min^{-1} (Fig. 2). An oronasal mask aperture ensured air pressure equilibration across the cheeks. Vertical displacement of the demand regulator provided air supply pressures equal to the hydrostatic pressure acting on the body surface within the range of mouth depth, to 27 cm below the sternal notch.

Respiratory gas samples were drawn through the chamber wall and analyzed for end-tidal carbon dioxide concentration (Beckman LB-2 CO_2 gas analyzer). Airway pressure recorded at the mouth (P_{ao}) was measured relative to the hydrostatic pressure at the regulator depth (Validyne MP45 ± 3.92 kPa). Heart rate was recorded directly from exercise electrocardiographs (Fuduka Denshi Electrocardiograph FD-13).

Air supply to the subjects was provided via the demand regulator from one of two calibrated cylinders, immersed in a water bath to control temperature fluctuations. At the end of each minute subjects were switched from one cylinder to the next by means of a high pressure, four-port valve, with cylinder pressures being recorded at the start and end of each minute (Celesco Transducer Production Inc., model PLD, ± 34 MPa). The cylinder not in use was refilled to a pressure of 13.8 MPa (2000 psi)

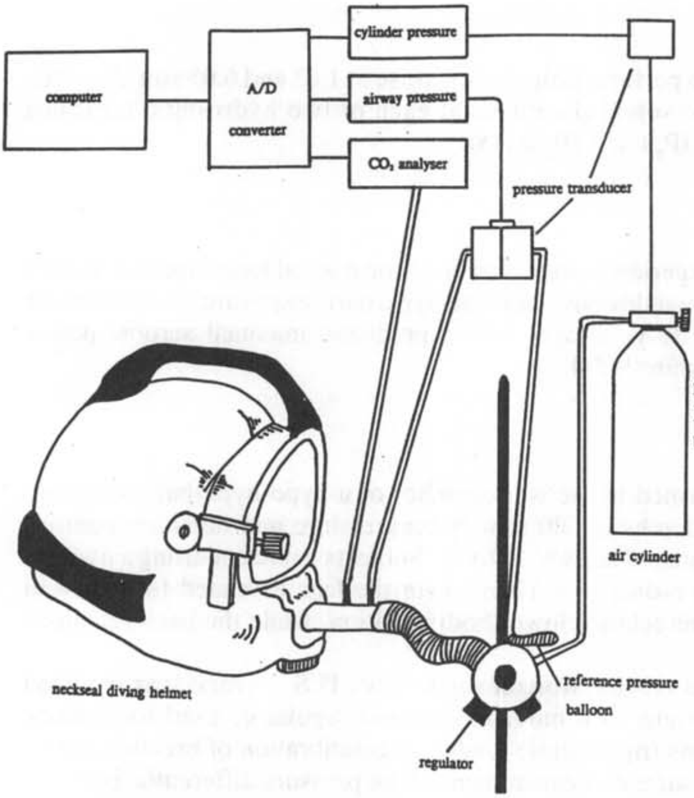

Fig. 1. Schematic of the modified neckseal diving helmet (Kirby Morgan super-light, U.S. Divers) used for all experiments.

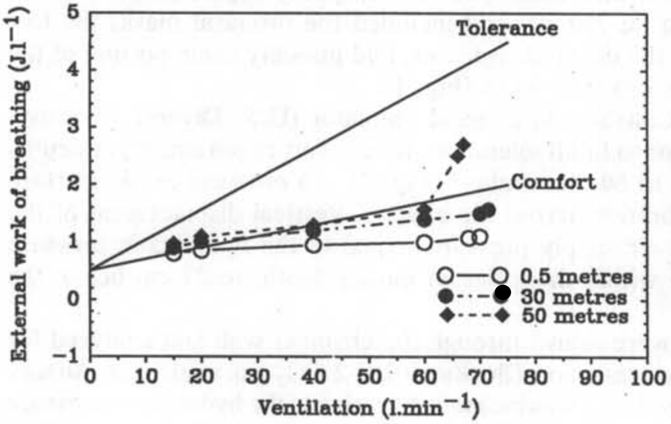

Fig. 2. External work of breathing using a Conshelf 30 (U.S. Divers) open circuit demand regulator at simulated depths of 0.5 to 50 m and over minute ventilations of 15 to 70 liters · min^{-1}. Data reproduced with permission from Morrison et al. (25).

from the master cylinder bank. A small surge bottle was positioned between the calibrated cylinders and the subject to prevent transient pressure drops at the regulator while switching cylinders. For immersions at 1.02 atm abs, 2.77-liter cylinders were used to enhance pressure measurement precision. At 6.05 atm abs, 11.1-liter cylinders were required to provide sufficient air during heavy exercise. The respective cylinder capacities were 0.566 m³ (20 ft³) and 2.27 m³ (80 ft³) of standard air at a working pressure of 21 MPa (3000 psi). Total air supply volumes, including cylinders, pressure hosing, and the surge bottle, were 3.68 and 12.01 liters for 1.02 and 6.05 atm abs experiments, respectively.

Pressure signals were amplified (Daytronic LVDT model 9130) and passed to a microcomputer (Digital Equipment Corp. LSI-11 03), via an analog-to-digital convertor (Digital Equipment Corp., LSI-11 RT-1251), for 50 Hz sampling and storage. Cylinder pressure and CO_2 gas fraction signals were similarly sampled and stored. A chart recorder (Hewlett Packard 7404A) provided on-line data inspection and backup.

Calibration was performed daily, or more frequently if the apparatus was shut down, or when large time gaps occurred between successive experiments. CO_2 analyzer calibration was performed at the flow rates encountered during testing to avoid delivery pressure biasing during gas analysis.

To evaluate power exerted against water resistance during limb movement, subjects pedaled at a constant frequency without load, in chin-depth water. After 5 min, a 1-min gas sample was collected and analyzed for CO_2 and O_2 concentration (Beckman LB-2 CO_2 gas analyzer, Ametek Applied Electrochemistry S-3A/I O_2 analyzer) and volume (American Meter Division, DTM-325 gas meter). The mean unloaded oxygen uptake ($\dot{V}O_2$) was 1.82 liter · min^{-1} STPD. Using the $\dot{V}O_2$ of each subject separately and assuming a 25% metabolic efficiency, the average unloaded resistive power was determined to be 153 ± 6 W. The ergometer was calibrated by measuring the relationship between hydraulic load (MPa) and crank torque (Nm). The relationship between fluid pressure and torque was linear (r = 1.00). Pedal frequencies were adjusted for each subject so that volitional fatigue was achieved within 10 min when a 1-min incremental protocol was used. At each increment of hydraulic load, power output was obtained from the sum of unloaded and ergonometric power.

Procedures

Each subject took part in five immersed training trials at 1.02 ATA before commencing the experimental dives. Subjects were asked to rate respiratory comfort each minute using a scale from zero to five (Table 1). During the final training trial, subjects rated comfort when the regulator was randomly and covertly positioned at mouth

TABLE 1
SUBJECTIVE RATING SCALE FOR PERCEIVED RESPIRATORY DISCOMFORT

Scale	Verbal Equivalent	Meaning
0	very, very light	just noticeable
1	light	very little effort, easy to breathe
2	moderate	at the limit of comfort, would prefer no greater
3	heavy	hard but acceptable
4	very heavy	at the limit of tolerance but could sustain
5	very, very heavy	very uncomfortable, interferes with breathing, could not sustain

level (P_m or uncompensated), P_{LC} level, and at 10 cm above and below lung centroid. Rating took place at rest, and cycling at a mean total power output of 280 ± 23 W. Lung centroid position was taken at 13.6 cm below the sternal notch (15).

Experimental trials were conducted on submerged subjects at ambient pressures of 1.02 and 6.05 atm abs, representing simulated seawater depths of 0.5 and 50.5 m at the level of the P_{LC} (subjects were approximately 0.5 m below the water surface, and the laboratory was about 300 m above sea level). Subjects breathed air at each of two air-supply pressures (P_m and P_{LC}) for both the 0.5- and 50.5-m dives. Subjects started each trial with a 1-min rest, then cycled at a constant pedal frequency against an increasing hydraulic load until fatigued, or until 10 min had elapsed. Work rate was incremented by adjusting hydraulic pressure at the end of each minute. The dive tender prompted signaling for perceived respiratory comfort at the end of each minute, CO_2 and P_{ao} signals were sampled continuously, ECG traces were taken over the last 10 sec of each minute, and cylinder pressure was sampled at the beginning and end of each minute. Subjects were instructed that they were free to terminate experiments at any point due to fatigue, respiratory discomfort, narcosis, or anxiety due to any cause.

Analysis

Analysis was based on a repeated measures experimental design containing two within-subjects factors (experimental condition and workload). Perceived respiratory discomfort rating was regarded as parametric data. A priori probability significance was set at the 0.05 level. Multivariate analysis of variance was used to search for significant interactions between experimental conditions and workloads. Analysis was also performed using a paired model following the attainment of a significant overall *F* statistic (Hotelling's T-squared correlated), because variability among subjects was large whereas changes between conditions were consistently in the same direction. Paired comparisons were made at each work rate, and for the combined data of all work rates, to search for differences between data obtained at 1.02 and 6.05 atm abs and for differences when breathing air supplied at P_{LC} and P_m.

RESULTS

Physical characteristics of subjects, exercise durations, and actual external work rates for each of the experimental conditions are detailed in Tables 2 and 3.

Using the respiratory discomfort rating scale, subjects evaluated comfort at four air-supply pressures at rest and while cycling at a mean total power output of 280 W. At all breathing pressures subjects perceived respiration to be significantly more comfortable ($P < 0.05$) at rest than during exercise (Fig. 3).

Analysis of the combined exercise and resting data showed that differences in perceived discomfort between P_{LC} and P_{LC} − 0.98 kPa air delivery were not significant ($P > 0.05$). However, subjects perceived respiration to be significantly more comfortable at these air supply pressures than at either P_m or P_{LC} + 0.98 kPa ($P < 0.05$).

During the incremental exercise trials some subjects were unable to complete the required 10-min protocol. Table 2 summarizes the exercise durations for all conditions. When immersed at 1.02 atm abs, terminal power averaged 331.8 ± 26.9 W

TABLE 2
PHYSICAL CHARACTERISTICS AND EXERCISE DURATIONS OF SUBJECTS

Subject	Age, yr	Years Diving	Mass, kg	Aerobic power, liter · min⁻¹	Exercise duration, min: 1.02 atm abs P_m	1.02 atm abs P_{LC}	6.05 atm abs P_m	6.05 atm abs P_{LC}
1	27	13	70.7	4.70[a]	10	10	7	10
2	24	2	81.5	4.75[a]	10	10	10	10
3	26	10	71.9	4.49[a]	10	10	8	9
4	23	1	71.7	4.80[a]	10	10	10	10
5	23	1	84.1	4.00	10	10	10	10
6	33	13	77.5	4.75[a]	9	9	7	7
7	27	1	82.0	4.41[a]	10	10	10	10
8	28	3	70.0	3.60[a]	10	10	10	8
9	26	5	75.4	3.90	10	10	10	9
10	26	4	89.3	3.70	10	10	10	10
Mean	26.3	5.3	77.4	4.31	9.9	9.9	9.2	9.3
SD	2.9	4.9	6.6	0.47	0.3	0.3	1.3	1.1

[a]Aerobic power measured using breath-by-breath analysis for a separate investigation conducted simultaneously, other values were predicted [Astrand-Rhyming prediction (24)].

TABLE 3
EXERCISE WORK RATES AND PEDAL FREQUENCIES FOR EACH SUBJECT[a]

Subject	Frequency	Exercise Time, min: 1	2	3	4	5	6	7	8	9	10
1	85	rest	179.5	200.8	222.1	243.4	264.6	285.9	307.2	328.5	342.7
2	80	rest	196.7	216.7	236.7	256.8	276.8	296.8	316.9	336.9	350.2
3	85	rest	182.5	203.8	225.0	246.3	267.6	288.9	310.1	331.4	345.6
4	85	rest	199.7	221.0	242.3	263.6	284.8	306.1	327.1	348.7	362.8
5	80	rest	205.1	225.1	245.1	265.1	285.2	305.2	325.2	345.2	358.6
6	70	rest	158.7	176.2	193.8	211.3	228.8	246.3	263.9	281.4	—
7	85	rest	163.0	184.3	205.5	226.8	248.1	269.4	290.6	311.9	326.1
8	75	rest	173.7	192.4	211.2	230.0	248.8	267.5	286.3	305.1	317.6
9	80	rest	141.2	161.2	181.2	201.3	221.3	241.3	261.3	281.4	294.7
10	75	rest	194.4	213.2	232.0	250.8	269.5	288.3	307.1	325.9	338.4

[a]Work rates are expressed in watts, and pedal frequencies are in revolutions per minute. *Note:* Within subject work rates were identical for each experimental condition. The final work rate for subject 6 is omitted because that subject failed to complete the 10-min exercise protocol on each trial. Refer to Table 2 for actual exercise durations for each subject during each experimental trial.

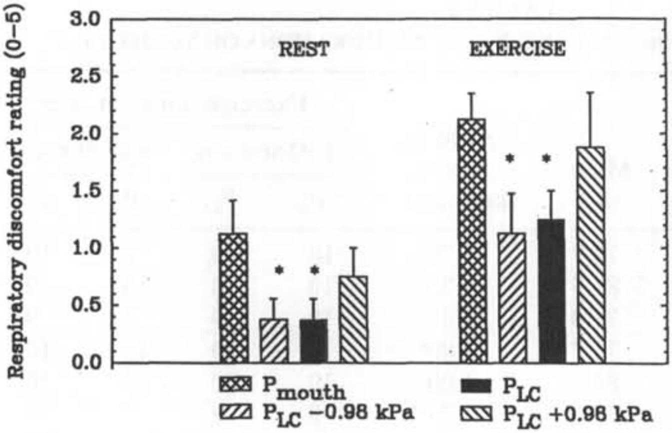

Fig. 3. Perceived respiratory discomfort at four breathing pressures with subjects resting and cycling at 280 W. Data represent means and standard error of the mean. Asterisk = significantly different from ratings obtained in the uncompensated state.

(terminal $\dot{V}O_2$ = 4.25 liter · min^{-1} including resting $\dot{V}O_2$) for both air supply pressures. At 6.05 atm abs, terminal power was 319.1 ± 36.4 W ($\dot{V}O_2$ = 4.10 liter · min^{-1}) and 322.4 ± 38.3 W ($\dot{V}O_2$ = 4.14 liter · min^{-1}) for P_m and P_{LC} air supply pressures, respectively. These differences were not significant ($P > 0.05$).

During incremental exercise trials subjects consistently perceived respiration to be more comfortable for all levels of exercise, and at both diving depths when the regulator was positioned at lung centroid depth (Fig. 4). Both at 1.02 and 6.05 atm abs subjects rated respiration at the final minute of exercise as "hard but acceptable" when breathing at P_m, and at the "limit of comfort" when breathing at P_{LC}. (Overall MANOVA $F = 6909.23$ (5,75), $P < 0.05$; for perceived respiratory discomfort, heart rate, minute ventilation, and end-tidal P_{CO_2} across work rate, absolute pressure, and gas delivery pressure.)

The paired data for all levels of exercise were examined for differences in respiratory discomfort associated with a change in absolute pressure and for differences associated with altered air delivery pressure. Subjects perceived respiration to be significantly less comfortable at 6.05 atm abs than at 1.02 atm abs ($P < 0.05$), while rating P_{LC} air provision to be more comfortable than uncompensated air supply ($P < 0.05$). This latter trend was apparent during trials at both absolute pressures (Fig. 4).

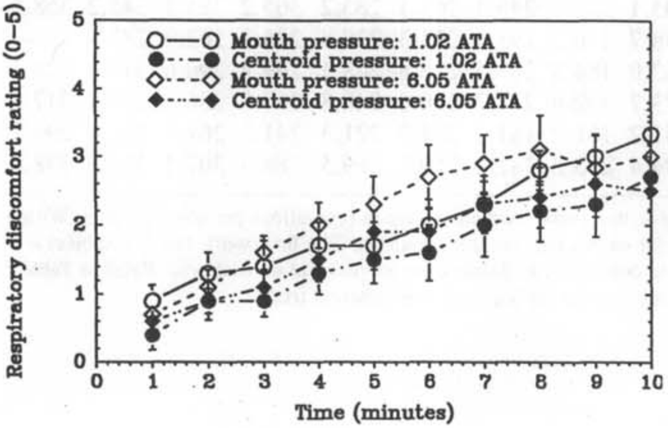

Fig. 4. Perceived respiratory discomfort during incremental exercise at 1.02 and 6.05 atm abs, with air delivered at P_m and P_{LC}. Data represent means and standard errors of the mean.

All subjects were questioned after each dive to obtain subjective reports concerning overall comfort, to identify reasons for failure to complete the exercise protocol, and to assess the magnitude of perceived narcosis. Several subjects ceased exercising prematurely due to volitional fatigue during the 1.02- and 6.05-atm abs trials; however, no subjects terminated exercise on the basis of either dyspnea or perceived respiratory fatigue. At 6.05 atm abs, 5 subjects chose to stop exercising because the level of narcosis was perceived to be either too unpleasant or a threat to consciousness.

When questioned after completing the 6.05-atm abs dives, 7 subjects reported feeling better when breathing air at P_{LC}. They reported being less narcotic, more aware of the physical work intensity and passage of time, and had better recall of events upon completion of the trial. At P_m air provision, 5 subjects reported visual, auditory, and mental aberrations; 2 of these subjects had to be helped off the cycle and 4 reported impending loss of consciousness. All symptoms disappeared immediately when the helmet was removed. Only 1 subject perceived narcosis to be greater when breathing air at P_{LC}.

Minute ventilation (VI) was significantly lower at 6.05 atm abs relative to 1.02 atm abs when data were compared across work rates and breathing pressures (Fig. 5) ($P < 0.05$). VI was significantly greater when breathing air supplied at P_{LC} relative to P_m when data were compared across work rates and absolute pressures (Fig. 5) ($P < 0.05$). This trend was primarily attributed to differences observed at 6.05 atm abs, where VI with air supplied at P_{LC} exceeded VI observed with air provision at P_m for all work rates. These differences were significant for work rates beyond Minute 3 ($P < 0.05$). Similar differences were not apparent at 1.02 atm abs.

Resting PET_{CO_2} at 1.02 atm abs averaged 38.4 and 38.5 mmHg for P_m and P_{LC}, respectively (Fig. 6). During 1.02 atm abs trials PET_{CO_2} followed a typical inverted-U relationship. At 6.05 atm abs PET_{CO_2} continued to rise throughout the course of the experiments for all except 1 subject. Subjects terminated exercise with an average PET_{CO_2} of 62.7 and 62.6 mmHg for P_m and P_{LC} air delivery, respectively (Fig. 6). Differences between PET_{CO_2} at 1.02 and 6.05 atm abs were significant ($P < 0.05$). Differences between PET_{CO_2} for the two air supply pressures were also significant when paired data were analyzed collectively ($P < 0.05$). The latter observation resulted from greater PET_{CO_2} during exercise at 1.02 atm abs when air was provided at P_{LC}. Although not significant, the PET_{CO_2} tended to be greater at 6.05 atm abs when

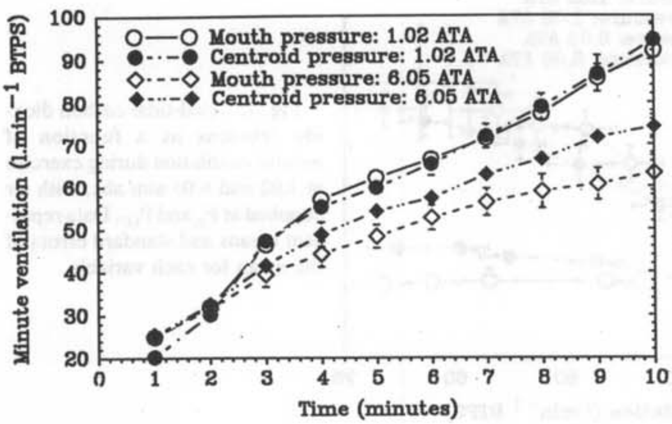

Fig. 5. Minute ventilation during incremental exercise at 1.02 and 6.05 atm abs with air delivered at P_m and P_{LC}. Data represent means and standard errors of the mean.

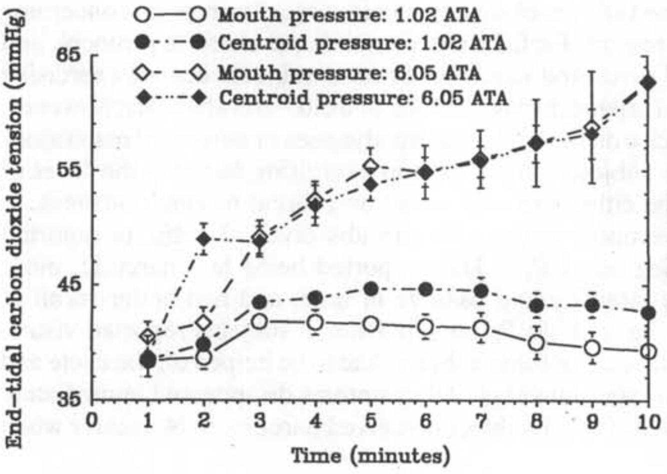

Fig. 6. End-tidal carbon dioxide tensions during exercise at 1.02 and 6.05 atm abs, with air delivered at P_m and P_{LC}. Data represent means and standard errors of the mean.

air was supplied at P_m. Differences between $P_{ET_{CO_2}}$ measurements at each air supply pressure at 6.05 atm abs were more pronounced when expressed as a function of minute ventilation (Fig. 7), so that at approximately equal ventilatory rates subjects seemed to experience greater hypercapnia when breathing air supplied at P_m. However, these differences were not significant ($P > 0.05$).

Significant bradycardia was observed at 6.05 atm abs relative to data at 1.02 atm abs ($P < 0.05$). Heart rates with P_m air provision were generally higher than observed when breathing air at P_{LC}. When analyzed collectively across work rates and absolute pressures, the mean difference was 5 beats · min^{-1} ($P < 0.05$).

Measures of perceived breathing discomfort, heart rate, and end-tidal CO_2 tensions were also compared at matched minute ventilations. At 1.02 atm abs these variables were not significantly different for P_m and P_{LC} air delivery ($P > 0.05$). [Overall MANOVA $F = 9859.73$ (4,86), $P < 0.05$; for perceived respiratory discomfort, heart rate, and end-tidal P_{CO_2} at 1.02 atm abs across matched minute ventilations and breathing pressures. Power of each statistic at 1.02 atm abs was 0.65, 0.55, and 0.11,

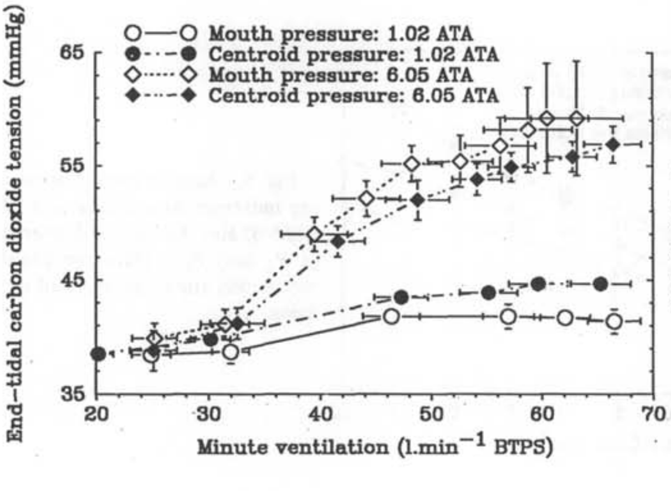

Fig. 7. End-tidal carbon dioxide tensions as a function of minute ventilation during exercise at 1.02 and 6.05 atm abs, with air supplied at P_m and P_{LC}. Data represent means and standard errors of the mean for each variable.

respectively.] At 6.05 atm abs, comparisons between data measured at P_m and P_{LC} air delivery revealed significant differences in perceived breathing discomfort (Fig. 8) and heart rate (Fig. 9), both when data were analyzed collectively across matched ventilations and at selected levels of ventilation ($P < 0.05$). (Overall MANOVA $F = 3772.83$ (4,55), $P < 0.05$; for perceived respiratory discomfort, heart rate, and end-tidal P_{CO_2} at 6.05 atm abs across matched minute ventilations and breathing pressures.) Breathing at P_{LC} was significantly more comfortable at matched minute ventilations of 42.5, 47.9, 57.4, and 61.9 liter · min^{-1} (Fig. 8) ($P < 0.05$). Heart rates at 6.05 ATA were significantly lower when breathing air supplied at P_{LC} for matched minute ventilations in excess of 40 liter · min^{-1} (Fig. 9) ($P < 0.05$).

DISCUSSION

While normobaric power is usually limited by cardiovascular mechanisms, many subjects, unless highly motivated, do not reach workloads where the cardiovascular system becomes a limitation. Subjects may stop due to local fatigue, general unpleasantness, and perceived maximal effort. Subjects vary considerably on threshold

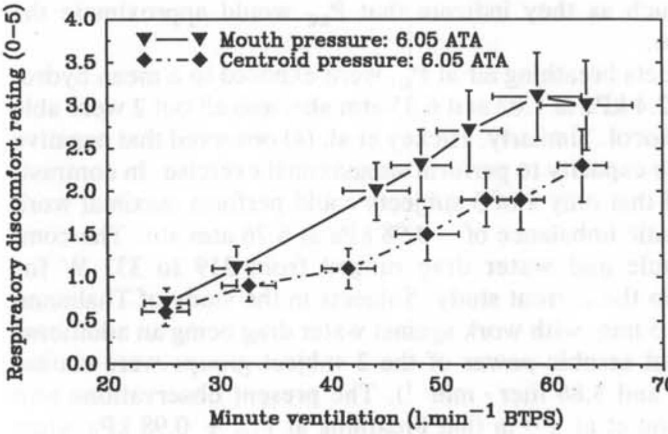

Fig. 8. Perceived respiratory discomfort for matched minute ventilations during incremental exercise at 6.05 atm abs, with air delivered at P_m and P_{LC}. Data represent means and standard errors of the mean.

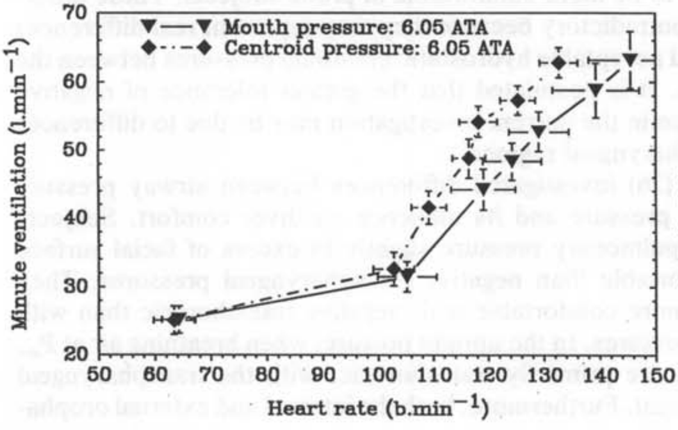

Fig. 9. Heart rates for matched minute ventilations, using air delivered at P_m and P_{LC} at 6.05 atm abs. Data represent means with standard errors of the mean.

levels for terminating exercise, possibly as a function of previous experience. It is possible that immersed exercise at 6.05 atm abs may alter the importance of these sensations, with changes in gas density elevating the role of respiratory comfort in exercise tolerance.

Dyspnea is associated with respiratory perturbations occurring during rest or exercise, which cause a mismatch between the demanded and obtainable ventilation. The subjects in this study reported breathing air at P_{LC} and $P_{LC} - 0.98$ kPa to be significantly more comfortable than breathing air at P_m or $P_{LC} + 0.98$ kPa during both rest and heavy, steady-state exercise at 1.02 atm abs (Fig. 3). During incremental exercise at 1.02 and 6.05 atm abs, breathing air supplied at P_{LC} was similarly perceived to be more comfortable than breathing air at P_m (Fig. 4). Results indicate that the provision of air at P_{LC} is preferable during upright, hyperbaric immersion because it reduces dyspneic sensations during heavy exercise.

Thalmann et al. (5) investigated underwater work in the prone position using positive and negative hydrostatic breathing loads (relative to the center of the thorax). They reported a tendency toward greater dyspnea at negative static loads. Direct comparison between this work and the current study is not possible because Thalmann et al. (5) used only 3 subjects, without statistical analyses, and used only a two-point dyspneic scale. The current results are to some extent in accord with those of Thalmann et al. (5), inasmuch as they indicate that P_{LC} would approximate the preferred air supply pressure.

In the present study, subjects breathing air at P_m, were exposed to a mean hydrostatic imbalance of about -2.4 kPa at 1.02 and 6.05 atm abs, and all but 2 were able to complete the exercise protocol. Similarly, Hickey et al. (4) observed that negative static loading did not alter the capacity to perform submaximal exercise. In contrast, Thalmann et al. (5) reported that only 1 of 3 subjects could perform maximal work when breathing at a hydrostatic imbalance of -0.98 kPa at 6.76 atm abs. The combined work against the cycle and water drag ranged from 319 to 332 W for the final minute of exercise in the current study. Subjects in the study of Thalmann et al. (5) averaged 246 W for 5 min, with work against water drag being an additional 23–25 W. The mean maximal aerobic power of the 2 subject groups were similar ($\dot{V}O_{2_{max}}$ = 4.31 liter · min^{-1} and 3.86 liter · min^{-1}). The present observations also differ from those of Thalmann et al. (5) in that breathing at $P_{LC} + 0.98$ kPa when upright was perceived to be less comfortable, whereas Thalmann et al. (5) reported positive pressure breathing to be more comfortable in prone subjects. These differences are not necessarily contradictory because they may represent real differences in pulmonary mechanics and acceptable hydrostatic breathing pressures between the upright and prone postures. It is postulated that the greater tolerance of negative breathing pressure imbalance in the current investigation may be due to differences in pressure across the oropharyngeal regions.

Thompson and McCally (26) investigated differences between airway pressure and oropharyngeal surface pressure and its influence on diver comfort. Subjects consistently found an intrapulmonary pressure slightly in excess of facial surface pressure to be more comfortable than negative transpharyngeal pressures. They found their subjects were more comfortable with negative transthoracic than with negative transpharyngeal pressures. In the upright posture, when breathing air at P_m, negative pressure gradients are primarily transthoracic, with the transpharyngeal pressure gradient being minimal. Furthermore, both the internal and external oropharyngeal surfaces were held at the same hydrostatic pressure in the current investigation. These conditions may explain the greater tolerance of negative pressure breathing observed in the present subjects, as compared with the observations of Thalmann et al. (5).

Morrison and Reimers (27) have prescribed physiologic specifications for underwater breathing apparatus and have provided recommended limits of comfort and tolerance for the work of breathing performed on such apparatus. The current open-circuit demand regulator conformed to the tolerance specifications for ventilations of 60 liter · min^{-1} at depths of 50 m. When divers breathed air at P_{LC}, the mean respiratory discomfort rating did not exceed 2.3. This corresponded with subjects reaching their limit of breathing comfort (Table 1). In this situation the combined internal and external respiratory work did not impose undue discomfort on the divers for ventilations up to 72 liter · min^{-1}. However, when divers were provided with air at P_m respiratory discomfort exceeded 2.9 for minute ventilations above 55 liters · min^{-1}. This rating indicated that divers perceived respiratory effort as heavy but acceptable. The difference between comfort ratings at the two air supply pressures reflects changes in the internal contribution to total respiratory work. With the Conshelf 30 regulator, the total work was within the limits of tolerance. However, with a demand regulator that requires greater external respiratory work, the combined internal and external flow-resistive and static work may impair ventilation. This may imply, for divers working upright and using mouth-held demand regulators, that the specifications of Morrison and Reimers (27) are not stringent enough at higher ventilations unless the apparatus provides for breathing pressure compensation as suggested by Taylor et al. (18).

Ventilatory reductions observed during hyperbaric exercise have been attributed to increased inspired O_2 tensions (28–30), reduced anaerobiosis (31), and increased airway resistance (8, 32). The current comparisons between $\dot{V}_I$ at different absolute pressures and the same air delivery pressure support these earlier observations. However, at 6.05 atm abs when breathing air at P_m, $\dot{V}_I$ diminished to a greater extent than when breathing air supplied at P_{LC}, and implies a possibly greater ventilatory impedence. This observation is contrary to the trend reported by Hickey et al. (4) who did not find an influence of static lung loading on minute ventilation during constant submaximal exercise. The present experiment was designed to provide subjects with approximately equivalent feed-forward (exercise-dependent) respiratory drive for each breathing pressure at 6.05 atm abs. Although respiratory drive was not quantified, it is clear that the combined exercise, chemoreceptor, and respiratory loading-dependent drive did not produce equivalent ventilations. Doell et al. (33) demonstrated that equivalent hypercapnic respiratory drive results in equivalent minute ventilation only when respiratory mechanics remain constant. They found that a gas-density elevation reduced ventilatory response to CO_2 by increasing airway resistance. Thus equivalent drive resulted in smaller minute ventilations. This observation may be applied to the current density-dependent ventilatory reduction observed when the absolute pressure was elevated. However, a second ventilatory reduction was seen when subjects breathed air at P_m at 6.05 atm abs (Fig. 5). The magnitude of the latter change was approximately equivalent to the reduction attributable to raised gas density for all but the final 2 min of exercise. Inasmuch as Morrison et al. (23) have shown that uncompensated immersion significantly increases pulmonary resistance, it is concluded that differences in pulmonary resistance between the two air delivery pressures caused the additional mechanical lowering of minute ventilation. This change was possibly due to dynamic airway compression accompanying increments in airway resistance.

The mechanical perturbations associated with breathing a dense gas supplied at P_m during immersion may reach the levels found in patients with respiratory disorders (e.g., chronic obstructive pulmonary disease). If this occurs, divers could experience a respiratory limitation of physical work capacity not unlike that observed in patients (34). However, this was not observed in the current study. At 6.05 atm abs the reduction of ventilation may have been compensated for by an increased inspired O_2 tension.

Perhaps of greater pertinence to diver safety than the possible ventilatory limitation of aerobic power is the retention of CO_2. Carbon dioxide has been shown to potentiate narcosis (35–37). In the present investigation exercise at depth was accompanied by a progressive CO_2 retention. While the current PET_{CO_2} changes may not quantify those expected with conventional breathing apparatus, due to the additional but constant respiratory dead space of the experimental apparatus, one would expect qualitatively similar trends during exercise performed at similar absolute pressures and breathing pressures.

Seventy percent of the current divers experienced more severe symptoms of narcosis when air was supplied at P_m. If CO_2 potentiation caused this change one would expect to observe a lower minute ventilation and a greater PET_{CO_2} at equivalent work rates. Minute ventilations were significantly lower for P_m air supply (Fig. 5) but, like the data of Hickey et al. (4), the changes in PET_{CO_2} were approximately equivalent for both air supply pressures at 6.05 atm abs (Figs. 6 and 7). This disparity is seen more clearly when PET_{CO_2} is expressed as a function of minute ventilation (Fig. 7). When subjects were ventilating at equivalent rates, although driven by different external work rates, they yielded greater PET_{CO_2} when air was supplied at P_m ($P > 0.05$). Several explanations are possible for the apparent contradiction between perceived narcosis, PET_{CO_2}, and minute ventilation. It is possible that gas sampling techniques may have been inadequate at 6.05 atm abs, although there is no evidence for this possibility. If one assumes that both the minute ventilation and PET_{CO_2} data are correct, then inequalities in tidal volume or breathing frequency or both may account for this difference. If upright immersion without compensation of the breathing pressure produced pulmonary changes similar to those encountered in elastic loading, then one would expect divers under these conditions to reduce their tidal volume while elevating their breathing frequency. Such a change might produce a lower PET_{CO_2} for a given minute ventilation and may explain the current data. However, in the absence of either tidal volume or breathing frequency data this possibility cannot be confirmed. Since subjects felt less comfortable with breathing air supplied at P_m, their perception of narcosis may have been negatively biased, producing spurious postexperimental reports. It is also possible that PET_{CO_2} may not have provided an accurate measure of arterial or cerebral CO_2 tension. In this situation the degree of CO_2 potentiation of narcosis would not be apparent from the PET_{CO_2} data.

Regardless of the cause, the degree of narcosis reported by the divers would indicate that, in the absence of breathing pressure compensation, the external work of breathing limits recommended by Morrison and Reimers (27) are not stringent enough for air diving to 50 m, particularly during upright heavy exercise.

It is concluded that upright immersion at 6.05 atm abs, without breathing pressure compensation, impairs exercise ventilation and adversely affects respiratory comfort. Both of these changes are attributed to increased pulmonary flow resistance accompanying hyperbaric, uncompensated immersion and may lead to reduced diver safety. It is suggested that underwater breathing apparatus be modified to provide air at a positive pressure of 1.33 kPa relative to the sternal notch (P_{LC}) when divers adopt an upright working posture, and that an equivalent pressure be applied to the external facial surfaces to ensure a pressure equilibrium across the oropharyngeal tissues.

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Experimental methods were approved by the Ethics Review Committee of Simon Fraser University. Decompressions adhered to the 1986 Canadian Forces Air Diving Tables (Table 2) and Procedures, and proceeded without incident.

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