

Contents

Preface

page xiii

Diving behavior

	1
1.1 Marine mammals	2
1.1.1 Pinnipeds: phocids	2
1.1.2 Pinnipeds: otariids	6
1.1.3 Pinnipeds: odobenids	8
1.1.4 Cetaceans	8
1.1.5 Sirenians	11
1.1.6 Marine carnivores	12
1.1.7 Aquatic mammals	12
1.2 Seabirds	12
1.2.1 Procellariiform seabirds	14
1.2.2 Charadriiform seabirds	15
1.2.3 Pelecaniform seabirds	16
1.2.4 Penguins	17
1.2.5 Other aquatic birds	20

Challenges of the breath hold and the environment

	22
2.1 Challenges in human breath-hold diving	22
2.1.1 Breath-hold duration "break point"	22
2.1.2 Shallow water black out	23
2.1.3 Oxygen storage	23
2.1.4 Carbon dioxide storage	24
2.1.5 Metabolic rate and the dive response	24
2.1.6 Pressure: gas laws	25
2.1.7 Pressure: barotrauma	25
2.1.8 Pressure: ambient pressure and heart rate	26
2.1.9 Pressure: nitrogen, decompression sickness and nitrogen narcosis	26
2.1.10 Pressure: high pressure nervous syndrome	27
2.2 Challenges of the environment	27
2.2.1 Challenges of the environment: pressure	27
2.2.2 Challenges of the environment: temperature and heat loss	28

2.2.3	Challenges of the environment: light	28
2.3	Sensory adaptations	29
2.3.1	Sensory adaptations: olfaction	29
2.3.2	Sensory adaptations: vision	29
2.3.3	Sensory adaptations: touch	30
2.3.4	Sensory adaptations: sound production	30
2.3.5	Sensory adaptations: hearing	31
3	Respiratory gas exchange	32
3.1	Marine mammal respiratory anatomy and function	32
3.1.1	Airway and lung anatomy in marine mammals	32
3.1.2	Respiratory mechanics in marine mammals	36
3.1.3	Lung volumes of marine mammals	37
3.2	Seabird respiratory anatomy and function	40
3.2.1	Airway, air sac, and lung anatomy in diving birds	40
3.2.2	Lung/air-sac volumes of diving birds	41
4	Oxygen storage and transport	44
4.1	Hemoglobin structure and function	45
4.2	O ₂ -hemoglobin dissociation curves	45
4.2.1	O ₂ -hemoglobin dissociation curves: marine mammals	47
4.2.2	O ₂ -hemoglobin dissociation curves: seabirds	47
4.3	Myoglobin structure and function	48
4.4	Calculation of O ₂ stores	50
4.4.1	Respiratory O ₂ stores	50
4.4.2	Blood O ₂ stores	51
4.4.3	Muscle O ₂ stores	58
4.5	Magnitude and distribution of total body O ₂ stores	63
4.6	Advantage of size in the rate of O ₂ store utilization	69
5	Cardiovascular dive response	71
5.1	Cardiovascular physiology in marine mammals	73
5.1.1	Blood flow distribution in terrestrial mammals at rest and during exercise	73
5.1.2	Forced submersions of seals: bradycardia and vasoconstriction	74
5.1.3	Forced submersions: angiography and Doppler flow probe measurements	75
5.1.4	Forced submersions: microsphere studies	76
5.1.5	Forced submersions: arterio-venous shunts	76
5.1.6	Forced submersion: the physiology and anatomy of peripheral vasoconstriction	77
5.1.7	Forced submersion: the physiology and anatomy of pulsatile myocardial blood flow	78

5.1.8	Forced submersion of other mammals	79
5.1.9	Simulated dives of pinnipeds	79
5.1.10	Trained submersions of pinnipeds: moderate bradycardia	79
5.1.11	Trained submersion: muscle blood flow during moderate bradycardias	80
5.1.12	Spontaneous breath holds and sleep apnea	81
5.1.13	Surface swimming: heart rate, cardiac output, and O ₂ consumption	83
5.1.14	Free dives: early studies of marine mammals	85
5.1.15	Weddell seals: heart rate and splanchnic/renal blood flows	85
5.1.16	Weddell seals: heart rate, myoglobin saturation and muscle blood flow	87
5.1.17	Weddell seals: heart rate and flipper stroke rate	88
5.1.18	Free dives: heart rates of other marine and aquatic mammals	89
5.1.19	Gray seals and elephant seals: heart rates during free dives	89
5.1.20	Elephant seals: venous oxygen profiles and blood flow implications	92
5.1.21	Stellar sea lions and California sea lions: heart rate during free dives	92
5.1.22	California sea lions: venous oxygen profiles and blood flow implications	94
5.1.23	Dolphins: heart rates during free dives	95
5.1.24	Other mammals: heart rates during free dives	96
5.1.25	Marine mammal cardiovascular response during free dives: summary	96
5.2	Cardiovascular physiology in seabirds	97
5.2.1	Forced submersions of birds: bradycardia and peripheral vasoconstriction	97
5.2.2	Simulated dives: birds	100
5.2.3	Surface swimming: birds	100
5.2.4	Free dives: birds	101
5.2.5	Free dives: ducks	101
5.2.6	Free dives: other flighted birds	102
5.2.7	Free dives: penguins	103
5.2.8	Free dives: recent studies of emperor penguins at an isolated dive hole	106
5.2.9	Heart rate and blood O ₂ profiles of emperor penguins: implications for blood flow	106
5.2.10	Muscle O ₂ profiles in emperor penguins: implications for muscle blood flow	107
5.2.11	Heart rate profiles of emperor penguins at sea	109
5.2.12	Avian cardiovascular responses during free dives: summary	110
5.3	Neuroregulation of the dive response in mammals and birds	111
5.3.1	Neuroanatomical pathways	111
5.3.2	Chemoreceptors in dabbling ducks	112
5.3.3	Higher cortical input	112

5.3.4	Reflex pathways in seals and diving ducks	112
5.3.5	Autonomic nervous system	113
5.3.6	Neuroregulation of the exercise response	114
5.3.7	Cardiovascular neuroregulation during dives	115
6	Adaptations in cardiovascular anatomy and hemodynamics	118
6.1	Marine mammals: the heart	118
6.2	Marine mammals: general vascular features and the spleen	119
6.3	Marine mammals: the extradural venous system of phocid seals	120
6.4	Marine mammals: thermoregulatory structures	121
6.5	Marine mammals: the aorta	122
6.6	Marine mammals: retia mirabilia	124
6.7	Marine mammals: vena caval and portal vein sphincters and the pericardial plexus	125
6.8	Diving birds: the heart	127
6.9	Diving birds: vascular anatomy	127
6.10	Hemodynamics	128
6.10.1	Bradycardia and myocardial oxygen supply/demand	128
6.10.2	Contractility and myocardial oxygen supply/demand	129
6.10.3	The caval sphincter, cardiac preload, and myocardial oxygen supply/demand	129
6.10.4	The aortic bulb, afterload, and myocardial oxygen supply/demand	130
6.10.5	Pulmonary vascular resistance and the right ventricle	130
6.10.6	Summary: hemodynamics and myocardial oxygen supply/demand	131
6.11	Avian hemodynamics	131
7	Muscle and locomotory work	133
7.1	Muscle fiber types	133
7.2	Muscle enzyme activities, energy substrates, and mitochondria	137
7.3	Locomotory work	139
7.3.1	Hydrodynamics and drag	140
7.3.2	Locomotory patterns and costs	142
8	Thermoregulation	145
8.1	Metabolism and heat production	146
8.2	Marine mammals: thermoregulatory anatomy and physiology	148
8.3	Marine mammals: body temperatures during dives	151
8.4	Marine birds: thermoregulatory anatomy and physiology	155
8.5	Marine birds: body temperatures during dives	158
9	Diving metabolism	162
9.1	Forced submersions and metabolic rate	162
9.2	Biochemical mechanisms of metabolic suppression	163

9.3	Basal and resting metabolic rates	165
9.4	Metabolic rate measurements	166
9.5	Diving metabolic rates: marine mammals	168
9.6	Diving metabolic rates: birds	170
9.7	Diving metabolic rates: summary	170
10	The aerobic dive limit	172
10.1	Aerobic dive limits determined by blood lactate measurements	172
10.2	Behavioral and calculated aerobic dive limits: indirect techniques	175
10.3	Physiological basis of the aerobic dive limit	176
11	Oxygen store depletion and hypoxemic tolerance	180
11.1	Oxygen store depletion in marine mammals	180
11.1.1	O ₂ depletion during forced submersions: seals	180
11.1.2	O ₂ depletion during sleep apnea: elephant seals	181
11.1.3	O ₂ depletion during free dives: elephant seals	184
11.1.4	O ₂ depletion during free dives: Weddell seals	187
11.1.5	O ₂ depletion during free dives: sea lions	188
11.1.6	O ₂ depletion in cetaceans: trained dives and stationary breath holds	190
11.2	Oxygen store depletion in seabirds	190
11.2.1	O ₂ depletion during forced submersions: penguins and ducks	190
11.2.2	Blood oxygen depletion during simulated dives: penguins	191
11.2.3	O ₂ depletion during free dives: emperor penguins	191
11.3	Blood gases, blood pH, and lactate	195
11.3.1	P _{O₂} , P _{CO₂} , and pH: forced submersion	196
11.3.2	P _{O₂} , P _{CO₂} , and pH: sleep apnea and stationary breath holds	197
11.3.3	P _{O₂} , P _{CO₂} , and pH: diving	197
11.3.4	Hypoxic and hypercapnic respiratory drives during diving	198
11.3.5	Blood lactate concentrations during and after dives	199
11.4	Mechanisms of hypoxemic tolerance	200
11.4.1	Hypoxemic tolerance: shorter O ₂ diffusion distances	200
11.4.2	Hypoxemic tolerance: neuroglobin	201
11.4.3	Hypoxemic tolerance: glycolytic and buffering capacities	202
11.4.4	Hypoxemic tolerance: hypothermia	203
11.4.5	Hypoxemic tolerance: hypoxia-linked mechanisms	203
11.4.6	Hypoxemic tolerance: avoidance of reperfusion injury	204
12	Pressure tolerance	205
12.1	Decompression sickness, nitrogen narcosis, and high-pressure nervous syndrome	205
12.1.1	Decompression sickness	206
12.1.2	Nitrogen narcosis and high-pressure nervous syndrome	206

12.2	Avoidance of barotrauma in marine mammals	207
12.3	Lung collapse and minimization of N ₂ absorption in marine mammals	209
12.4	Pulmonary shunts in marine mammals	211
12.5	Avoidance of decompression sickness in marine mammals	212
12.5.1	Avoidance of decompression sickness in marine mammals: thoracic rete hypothesis	213
12.5.2	Avoidance of decompression sickness in marine mammals: N ₂ supersaturation	214
12.5.3	Avoidance of decompression sickness in marine mammals: N ₂ solubility	214
12.5.4	Avoidance of decompression sickness in marine mammals: blood N ₂ levels	215
12.5.5	Avoidance of decompression sickness in marine mammals: summary	215
12.6	Cellular and biochemical effects of pressure in marine mammals	216
12.7	Sonar-associated whale strandings	216
12.7.1	Dive behavior	217
12.7.2	Anatomy, pathology, and physiology	218
12.7.3	Models of N ₂ uptake and distribution	219
12.8	Avoidance of barotrauma in diving birds	221
12.9	Avian lung structure and effects of pressure	221
12.10	Gas exchange in penguins at depth: pulmonary shunts and heart rate	223
12.11	Blood N ₂ levels in penguins	224
13	Bio-medical relevance	226
13.1	Avoidance of reperfusion injury and hypoxemic/ischemic tolerance	226
13.2	Lung surfactant function	229
13.3	Hypoxic pulmonary vasoconstriction	231
13.4	Regulation of myoglobin production	233
13.5	Myoglobin "biophysics"	236
	<i>References</i>	240
	<i>Index</i>	321