respiratory physiology of diving mammals

DMLS

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Runtime: 60 min
Slides: 70
## Hall of fame

<table>
<thead>
<tr>
<th>Animal</th>
<th>Time</th>
<th>Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>sperm whale</td>
<td>138 min</td>
<td>2250 m</td>
</tr>
<tr>
<td>elephant seal</td>
<td>120 min</td>
<td>1256 m</td>
</tr>
<tr>
<td>weddell seal</td>
<td>82 min</td>
<td>726 m</td>
</tr>
<tr>
<td>cal. sea lion</td>
<td>15 min</td>
<td>482 m</td>
</tr>
<tr>
<td>walrus</td>
<td>12 min</td>
<td>100 m</td>
</tr>
<tr>
<td>bottle nose dolphin</td>
<td>8 min</td>
<td>390 m</td>
</tr>
<tr>
<td>sea lion</td>
<td>8 min</td>
<td>250 m</td>
</tr>
<tr>
<td>fur seal</td>
<td>5 min</td>
<td>101 m</td>
</tr>
<tr>
<td>manatees</td>
<td>3 min</td>
<td>12 m</td>
</tr>
<tr>
<td>sea otter</td>
<td>2.3 min</td>
<td>23 m</td>
</tr>
<tr>
<td>homo sapiens (untrained)</td>
<td>1 min</td>
<td>?4 m</td>
</tr>
</tbody>
</table>


Ponganis PJ. Diving Mammals. Comp Physiol 2011;1:517-535

We are shallow divers
Human apnea divers

• competitive apnea diving (single dives)
  – Branko Petrovic  11:54  (static apnea)
  – Herbert Nitsch  253 msw  (no limits)
Commercial apnea divers

- commercial skindivers (repetitive within ADL)
  - Ama divers (Japan and Korea) average dive time: 38 sec with equal surface intervals, foraging at 5-12 msw
similar evolutionary adaptations in different species
Ambulocetus, an early cetacean that could walk as well as swim (45 million yrs ago)

Puijila darwini was a semi-aquatic carnivore (24 million yrs ago)
Evolution in progress?

excellent swimmer, 13 sec dives
Problems of diving when you are not a fish

- drag
- temperature homeostasis
- DCS
- N\textsubscript{2} narcosis
- O\textsubscript{2} toxicity
- barotrauma
- O\textsubscript{2} supply

streamlining
insulation & size
Big, fat or furry

- homeothermic endotherm
- heat conduction water vs air: x 25!
- conductive heat loss: \( SA \times C \times T \text{ grad} \)
  - \( SA = \) surface area
  - \( C = \) thermal conductance
  - \( T = \) temperature gradient

- insulation: blubber or fur
  
  low surface area/volume ratio
  
  insulation: blubber or fur
• only the densest fur maintains a layer of trapped air when wet
  – multiple underhairs per hair canal
  – fur seal: 60,000 hairs/ cm$^2$
  – sea otter: 130,000 hairs/ cm$^2$
  – hydrophobic liquid/ sebaceous
• air compression during deep dives!
Blubber

- insulation (not as efficient as dry fur)
  - fat content
  - thickness
- vascularised to enable heat loss
- energy store
- buoyancy
Problems of diving
when you are not a fish

- drag
- temperature homeostasis
- DCS
- $N_2$ narcosis
- $O_2$ toxicity
- barotrauma
- $O_2$ supply

streamlining
insulation & size
don’t breath!
• seals exhale before diving

• alveolar collapse (atelectasis)
  – total collapse at 25 - 50 msw (varies per species)

Flexible chest case
More cartilage
Reinforced terminal airways
Whales lack a sternum
Special surfactant with an anti-adhesive effect

Oblique diafragm

Manatee and Harbor seal
• bulging diafragm
• displacement of abdominal organs
• less flexible chest cage
• lung squeeze!
• theoretical ‘MOD’: at residual lung volume

\[(\text{TLC:RV} + 1) \times 10 = \text{MOD in msw}\]
\[
\begin{align*}
\text{TLC} &= 8 \\
\text{RV} &= 0.5 \\
\text{MOD} &= 170 \text{ msw}
\end{align*}
\]
Tricks of the trade

- Lungpacking
  - Buccal pumping, TLC + 2 L
  - Increased inspiratory reserve volume
- Reversed lungpacking at depth
  - To decrease residual lung volume
  - 'Suck air from the lungs'
- Pliant diafragm
  - Allowing for displacement of abdominal organs

Schagatay E. Predicting performance in competitive apnea diving. Part II: depth. Diving and hyperbaric medicine 2011;41:216-228
Decreasing residual volume
Lung volumes

Lung packing

Pliant diafragm
Other respiratory adaptations

- (non humans)
- nares are closed, opening requires muscular contraction
- powerful laryngeal muscles
- cartilage reinforcement of terminal airways
  - so that the alveoli collapse before the trachea and bronchus.
  - prevent airway closure during expiration
Dynamic airway collapse

Dynamic ventilatory mechanics: *dynamic airway compression*

**Forced expiration:**

- **Closing volume**
- **Equal pressure point**
Blue whale: 1500 L in & expiration in 2 sec
90% air renewal in one breath! (humans 10%)
Total alveolar collaps in diving mammals at 25-50 msw protects against excessive nitrogen partial pressure and absorption
Dysbaric osteonecrosis in whales?

deltoid crest  
nasal bone  
sub-articular chevron bone surface
Problems of diving
when you are not a fish

- drag
- temperature homeostasis
- DCS
- $N_2$ narcosis
- $O_2$ toxicity
- barotrauma
- $O_2$ supply

- streamlining
- insulation & size
- don’t breathe!
- no airpockets
- a bit more complicated
Barotrauma

• narrowing of the proximal airways
• absence of air-filled sinuses
• expansible venous plexuses lining the middle ear cavity
• expansible venous sinuses in tracheal wall

trachea of the striped dolphin Stenella coeruleoalba
Limited $O_2$ supply

- Increase oxygen stores or
- decrease oxygen use!

- decreased temperature/ metabolic rate?
- decrease activity?
- anaerobic processes?
- increased oxygen storage?
Hypometabolism?

Harbour seal during experimental dive
A = brain, B = abdomen, C = dorsal musculature
**O₂ storage**

- **Weddel seal** 380 kg
  - Blood volume: 15%
  - Height: 50-60
  - **82 minutes**

- **Fur seal** 200 kg
  - Blood volume: 11%
  - Height: 50

- **Human** 70 kg
  - Blood volume: 7%
  - Height: 40
  - **1 minute**
weight 10.000 kg
blood volume 20%
Ht 52
myoglobin 56 gr/kg

68 ml $O_2$/kg
lungs 4%
blood 38%
muscle 58%

Kooyman GL, Ponganis PJ. The physiological basis of diving to depth: Birds and mammals. Annu Rev Physiol 1998;60:19-32
Mass whale hunting Faroe islands
**O_2** stores

- **lung**
  - Hb bound
    - $x$ 9.5 in whales
    - $P_{50} = 26$-30 mmHG
    - Hb correlates with max depth
  - myoglobin
    - $P_{50} = 3$ mmHG
    - Mb 10-30 x
- ‘scuba cylinders’:
  - spleen
  - retia mirabilis

Autotransfusion

Seal spleen:
- 4.5% of body weight
- correlates with dive depth

Oxygen and the diving seal. Thornton SJ, Hochachka PW. UHM 2004;31:81-93
Spleen contraction
• contorted spirals of blood vessels, arterial + venous
• blood reservoir (oxygen storage)
• to accommodate increased thoracic blood volume (peripheral blood shift)

Dive patterns

Dive Depth Comparisons

- Common Foraging Depths
- Maximum Dive Depth

#Seldom hunts at the surface
*May hunt to maximum depth.
**When hunting Pinnipeds.
Dive patterns

Summaries of depths, durations, and postdive intervals of over 36,000 dives made by six adult male northern elephant seals (error bars = ±1 s.e.). (Redrawn from DeLong and Stewart, 1991.)
Aerobic Dive Limit (ADL)
<table>
<thead>
<tr>
<th>Shallow divers + terrestrial</th>
<th>Deep divers</th>
</tr>
</thead>
<tbody>
<tr>
<td>• sea otter, fur seal, human</td>
<td>• weddel seal, whales</td>
</tr>
<tr>
<td>• inspiration before diving</td>
<td>• seals exhale before diving</td>
</tr>
<tr>
<td>• $O_2$ source storage = lung</td>
<td>• $O_2$ storage = Hb &amp; myoglobinine</td>
</tr>
<tr>
<td>• dive within ADL</td>
<td>• most dives &lt; ADL</td>
</tr>
<tr>
<td></td>
<td>• can go beyond ADL</td>
</tr>
</tbody>
</table>

Snyder GK. Respiratory adaptations in diving mammals. Resp Physiol. 1983;54:269-294
• during 2 months at sea
• 85% of time under water
• average depth 400 m
• average dive time 20 min (ADL)
• surface interval 3 min
• frequent ADL dives are the most efficient (no oxygen debt)
Two big questions…..

• How to conserve oxygen?

• How to cope with lactate acidosis and hypoxia?
The mammalian dive response

- apnoe
- peripheral vasoconstriction
- centralisation of circulation
- reduced cardiac output
- bradycardia

- reduce $O_2$ consumption (activity is a factor)
- peripheral lactic acid accumulation
- reduced peripheral metabolism due to acidosis and hypothermia
 Redistribution

centralization

• brain
• retina
• lung
• heart

peripheral shutdown

• skin
• muscle
• splanchnic organs
AV anastomosis

Kooyman GL. Diverse divers: physiology and behavior. 1989 Springer-Verlag, Berlin
Redistribution Weddell seal

- Pancreas and liver
- Heart
- Lung
- Retina
- Cerebellum
- Cortex

Blood flow (ml min^{-1} g^{-1} tissue)
Metabolic depression

Core temperature is maintained!

Peripheral shutdown $\rightarrow$ Hypothermia $\rightarrow$ Acidosis $\rightarrow$ Local depressed metabolic rate
Bradicardia (seal)
Maintained MAP
Aortic bulb

- heart frequency down to 5%
- increased stroke volume
- aortic bulb & elastic recoil
- windkessel function

Ventral view of heart of Weddell seal
Ischemic tolerance

Accumulation of muscle lactate and oxygen depletion in harbor seals

Renal blood flow before and after 60 min of ischemia

• only in seals!
• to prevent venous return
• to titrate autotransfusion (spleen)
• to protect the heart against acidotic blood
Grey seal, experimental dive in captivity

O$_2$ debt
### Blood Gasses

<table>
<thead>
<tr>
<th>Weddell Seal</th>
<th>Duration</th>
<th>$PO_2$</th>
<th>$PCO_2$</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Free dive</td>
<td>27 min</td>
<td>18 mmHg</td>
<td>55 mmHg</td>
<td>7.3</td>
</tr>
<tr>
<td>Forced submersion</td>
<td>55 min</td>
<td>10 mmHg</td>
<td>84 mmHg</td>
<td>7.11</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Weddell Seal</th>
<th>Duration</th>
<th>$PCO_2$</th>
<th>pH</th>
<th>Lactate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forced submersion</td>
<td>61 min</td>
<td>post dive 55 mmHg</td>
<td>post dive 6.8</td>
<td>max 26 mmol/L</td>
</tr>
<tr>
<td>Free dive</td>
<td>&lt; ADL</td>
<td></td>
<td>max 2 mmol/L</td>
<td></td>
</tr>
</tbody>
</table>
Cerebral hypoxic tolerance

- maintained flow during bradycardia
- hypoxic tolerance down to $\text{PaO}_2$ 8 mm Hg in Harbour seal
- anaerobic metabolism!
- increased glycogen
- high capillary density

Kerem D, Elsner R. Cerebral tolerance to asphyxial hypoxia in the harbour seal. Respiration physiology 1973;19:188-200
Krogh cylinders

Capillary 30-60 µm from tissue cell
Initiation of dive response

- Immersion/ stimulation of the face, nasal mucosa and pharynx
  - cold > warm water
  - pain
- breath holding
- cessation of lung inflation
- synergistic response
Trigeminal nerve stimulation
Maintenance and termination

- hypoxia, hypercapnia and acidosis reinforce dive response
- activity level
- pulmonary inflation (ascend) terminates dive response
- conscious control!
  - variable bradycardia
  - modest dive response if voluntary shallow dive within ADL
all *vertebrates* exhibit a dive response.

- caiman from 28 > 2 beats/min.
- neural pathways are universal
  - sympathetic > vasoconstriction
  - parasympathetic > bradycardia
Bradycardia in free divers
• high pressure nervous syndrome in human divers possible > 15 atm
• occurs in all animals with a CNS
• animal life up to 1000 atm!
• unknown coping mechanism
• no data for diving mammals
• theory: alveolar muscular sfincter can allow for some N$_2$ absorption

Brauer RW. Hydrostatic pressure effects on the central nervous system:. Philosophical transactions of the royal society of london: series b, biological sciences.1984;304:17-30
Summary

• most dives within ADL
• variable dive response
• conscious control
• centralisation of circulation
• bradycardia
Summary

- **Physiologic adaptations:**
  - increased oxygen storage
  - (Ht, Blood volume, myoglobin, huge spleen, retia mirabilia)
  - compliant aorta/ bulging diafragm/ caval sfincter
  - reinforced terminal bronchi, special surfactant
  - hypoxic tolerance: brain, kidney and gut
  - glycogen stores, capillary density
### After thoughts

<table>
<thead>
<tr>
<th>Sign</th>
<th>Score = 0</th>
<th>Score = 1</th>
<th>Score = 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heart Rate</td>
<td>Absent</td>
<td>Below 100 Per Minute</td>
<td>Above 100 Per Minute</td>
</tr>
<tr>
<td>Respiratory Effort</td>
<td>Absent</td>
<td>Weak Irregular Or Gasping</td>
<td>Good, Crying</td>
</tr>
<tr>
<td>Muscle Tone</td>
<td>Flaccid</td>
<td>Some Flexion Of Arms And Legs</td>
<td>Well Flexed Or Active Movements Of Extremities</td>
</tr>
<tr>
<td>Reflex / Irritability</td>
<td>No Response</td>
<td>Grimace Or Weak Cry</td>
<td>Good Cry</td>
</tr>
<tr>
<td>Color</td>
<td>Blue All Over Pale</td>
<td>Body Pink Hands And Feet Blue</td>
<td>Pink All Over</td>
</tr>
</tbody>
</table>
Perinatal asphyxia

- polycythemia (diving mammals)
- channel dens, (hibernating turtles)
- hypothermia (hibernating turtles)
- bradycardia (diving mammals)
- redistribution (diving mammals)
- apnea (diving mammals)
- acidosis induced metabolic suppression (diving mammals)

Thank you for your attention!

Slides available at www.mattijnb.nl

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