Respiratory physiology of diving mammals

16-06-2018

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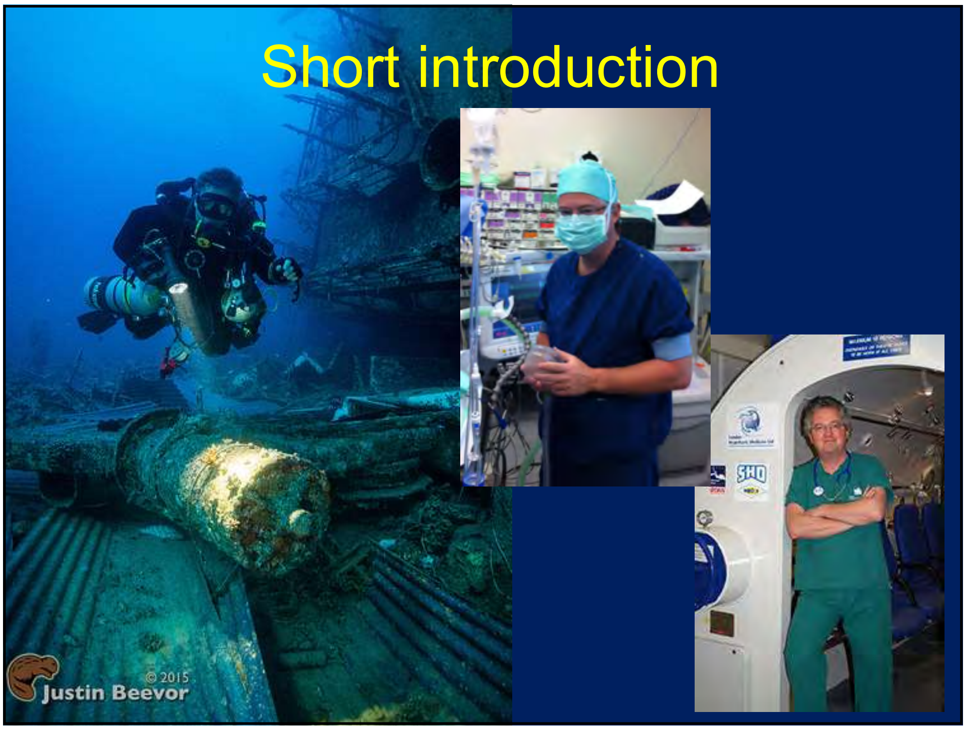


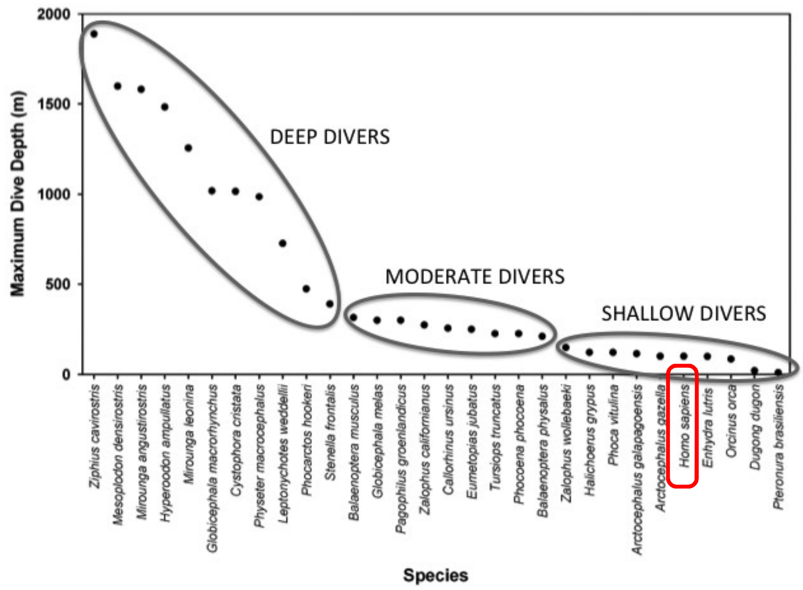
Seal nursery Pieterburen (NL)

Hall of fame

• sperm whale	138 min	2250 m
• elephant seal	120 min	1256 m
• weddell seal	82 min	726 m
• cal. sea lion	15 min	482 m
• walrus	12 min	100 m
• bottle nose dolphin	8 min	390 m
• sea lion	8 min	250 m
• fur seal	5 min	101 m
• manatees	3 min	12 m
• sea otter	2.3 min	23 m
• homo sapiens (untrained)	1 min	?4 m

Ponganis PJ. Diving Mammals. Comp Physiol 2011;1:517-535
Schagatay, E., Fahlman, A. Man's place among the diving mammals. Human Evolution. 2014;29(1-3): 47-66
Schreer, J. F., and K. M. Kovacs (1997). "Allometry of Diving Capacity in Air-Breathing Vertebrates." Can.. Zool. 75: 339–358

We are shallow divers

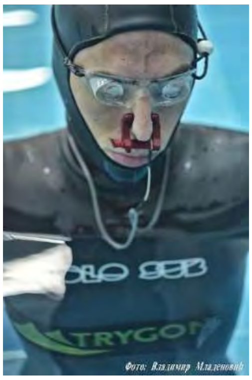


Schagatay, E., Fahlman, A. Man's place among the diving mammals. Human Evolution. 2014;29(1-3): 47-66

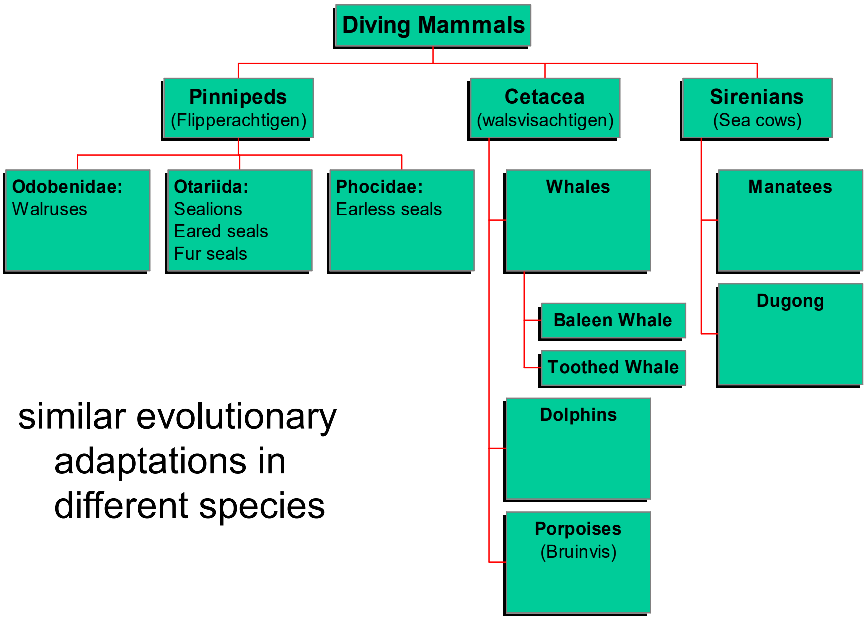
Baby divers

Human apnea divers

- competitive apnea diving (single dives)
  - Branko Petrovic 11:54 (static apnea)
  - Herbert Nitsch 253.2 msw (no limits)



'Family tree'



similar evolutionary adaptations in different species

Crawling back to sea

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

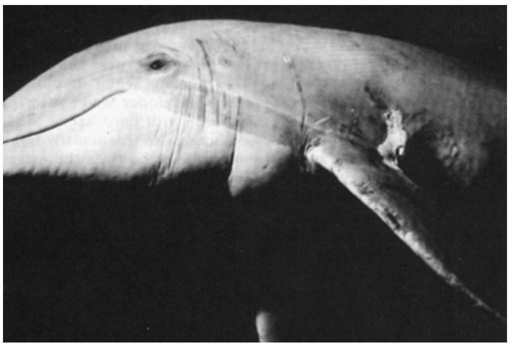
when you are not a fish

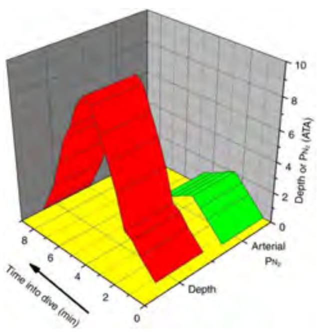
- drag → streamlining
- temperature homeostasis → insulation & size
- DCS
- N_2 narcosis
- O_2 toxicity

- barotrauma → no airpockets
- O_2 supply → a bit more complicated

Limit alveolar gas exchange

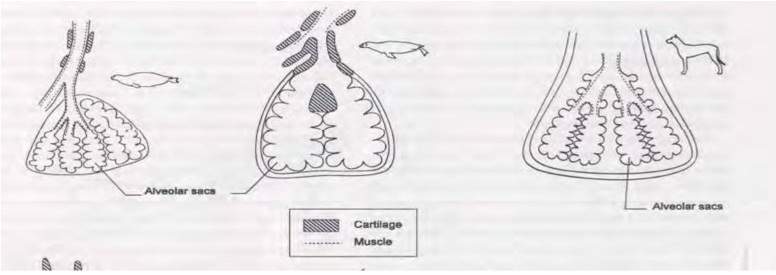
- seals exhale before diving
- alveolar collapse (atelectasis)
  - total collapse at 25 - 50 msw (varies per species)





Falke KJ, Hill RD, Qvist J, et al. Seal lungs collapse during free diving: evidence from arterial nitrogen tensions. Science. 1985 Aug 9;229(4713):556-8

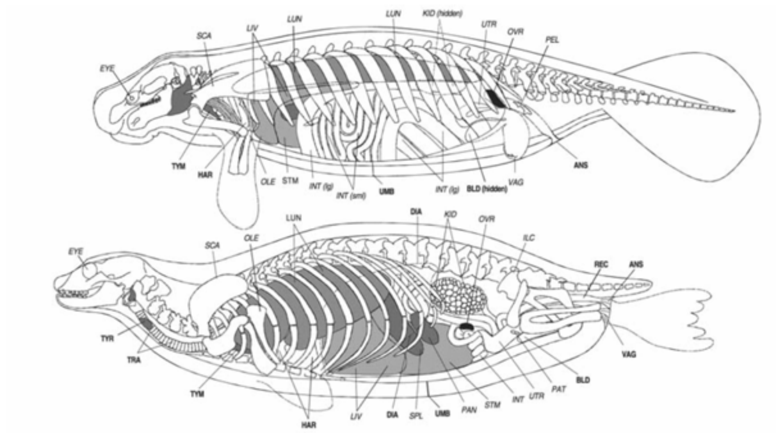
Pulmonary adaptations



- flexible chest case
- more cartilage
- reinforced terminal airways
- whales lack a sternum
- special surfactant with an anti-adhesive effect

Miller NJ, et al. The surface activity of pulmonary surfactant from diving mammals. Respir Physiol neurobiol 2006;150:220-32

Oblique diafragm



Manatee and Harbor seal

- bulging diafragm
- displacement of abdominal organs

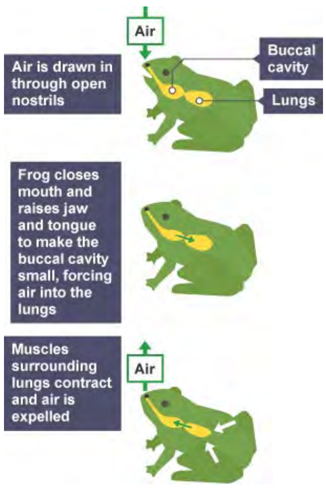
Lung collapse in humans

- less flexible chest cage
- lung squeeze!
- theoretical 'MOD': at residual lung volume

(TLC:RV +1) x 10 = MOD in msw
TLC = 8 RV = 0.5
MOD = 170 msw

Trics of the trade

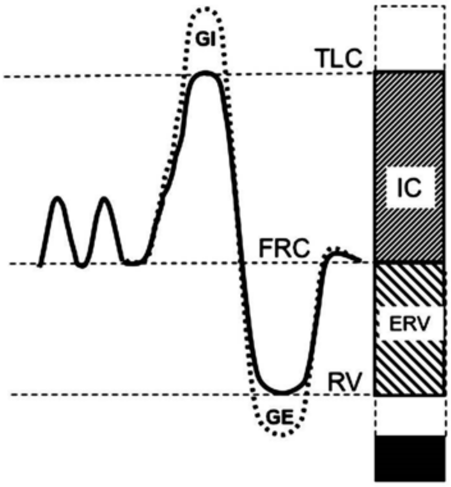
- lungpacking
  - buccal pumping, TLC + 2 L
  - increased inspiratory reserve volume
- pliant diafragm
  - allowing for displacement of abdominal organs



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

Decreasing residual volume

Lung volumes



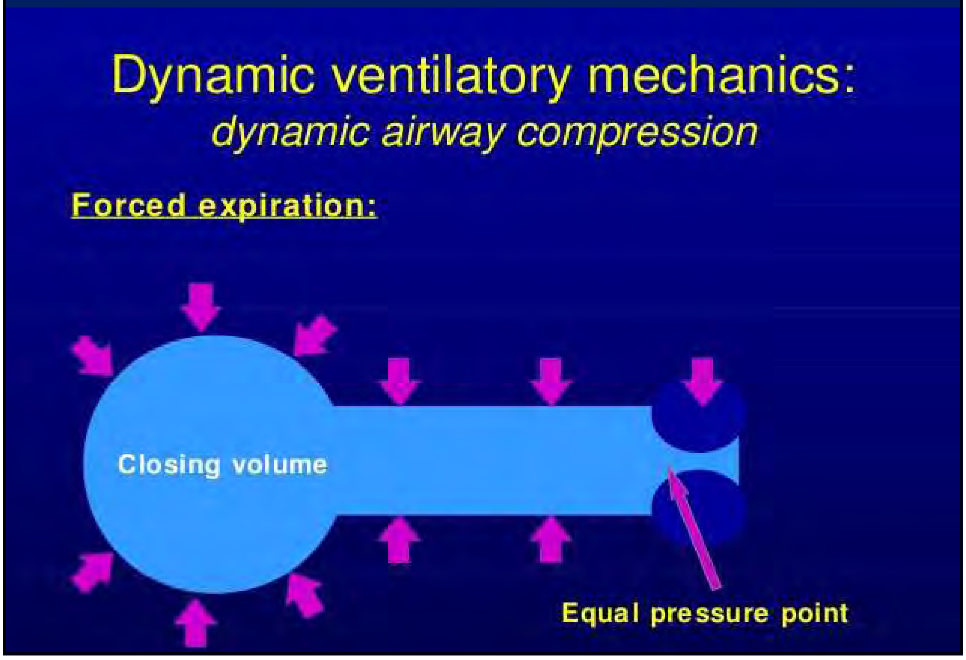
Lung packing

Pliant diafragm

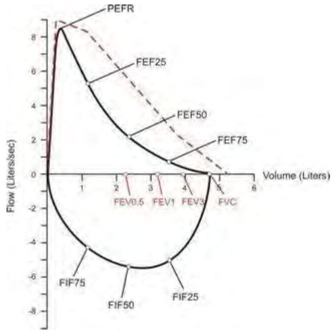
Other respiratory adaptations

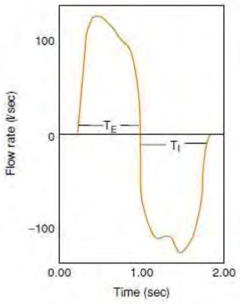
- (non humans)
- nares are closed, opening requires muscular contraction
- powerful laryngeal muscles
- cartilage reinforcement of terminal airways
  - so that the alveoli collapse before the trachea and bronchus.
  - prevent airway closure during expiration

Dynamic airway collapse



Expiration



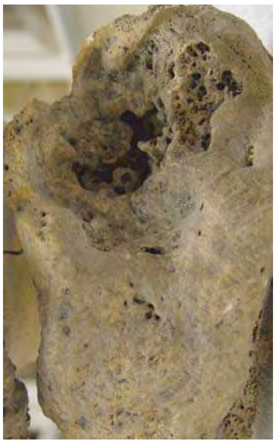


- Blue whale: 1500 L in & expiration in 2 sec
- 90% air renewal in one breath! (humans 10%)

Dysbaric osteonecrosis in whales?

deltoid crest

nasal bone

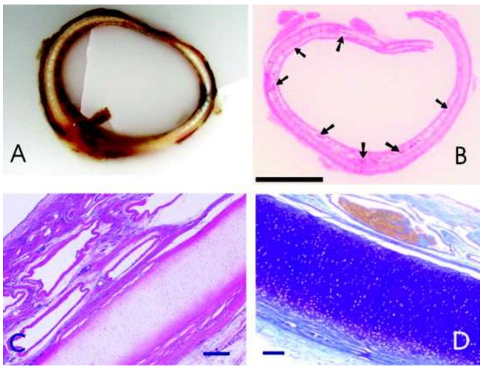


sub-articular chevron bone surface

Moor MJ, Early GA. Cumulative Sperm Whale Bone Damage and the Bends. Science 24 Dec 2004: Vol. 306, Issue 5705, pp. 2215

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

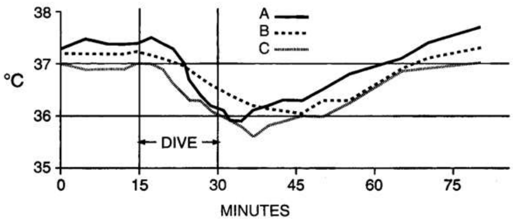


trachea of the striped dolphin Stenella coeruleoalba

The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology Volume 284A, Issue 1, pages 500-510, 24 MAR 2005 DOI: 10.1002/ar.a.20182
http://onlinelibrary.wiley.com/doi/10.1002/ar.a.20182/full#fig4

Limited O_2 supply

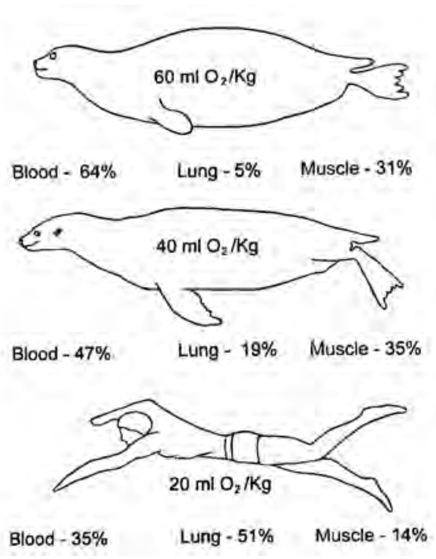
- Increase oxygen stores or
- decrease oxygen use!



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

Sholander PE, et al. On the temperature and metabolism of the seal during diving. J cell compar physiol. 1942;21:53-63

O_2 storage



Weddel seal 380 kg
Blood volume 15%
Ht 50-60

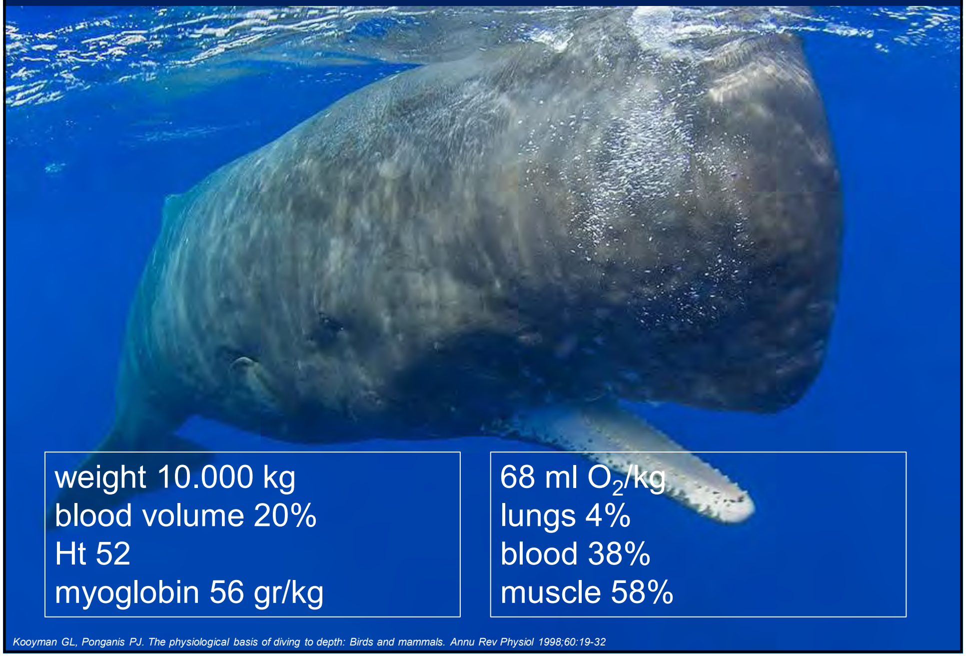
82 min

Fur seal 200 kg
Blood volume 11%
Ht 50

Human 70 kg
Blood volume 7%
Ht 40

1 min

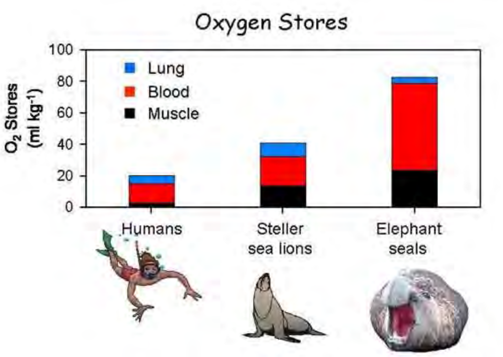
Sperm whale (physeter macrocephalus)



Mass whale hunting Faroe islands

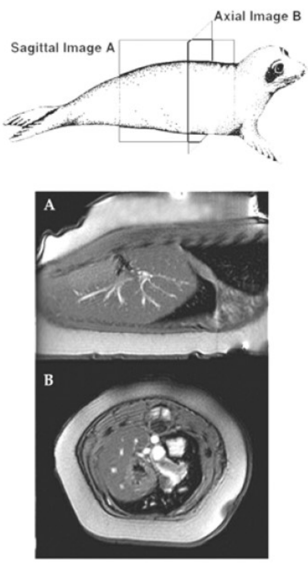
O_2 stores

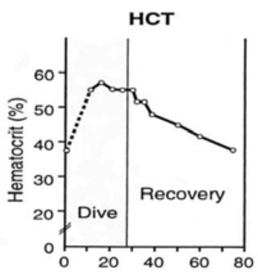
- lung
- Hb bound
  - x 9.5 in whales
  - P_{50} = 26-30 mmHG
  - Hb correlates with max depth
- myoglobin
  - P_{50} = 3 mmHG
  - Mb 10-30 x
- ‘scuba cylinders’:
  - spleen
  - retia mirabilis



Lenfant C.Physiological properties of blood of marine mammals. In: Anderson HT editor. The biology of marine mammals. New York:Academic press.1969.p.95-116

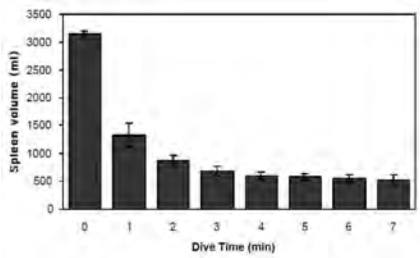
Autotransfusion





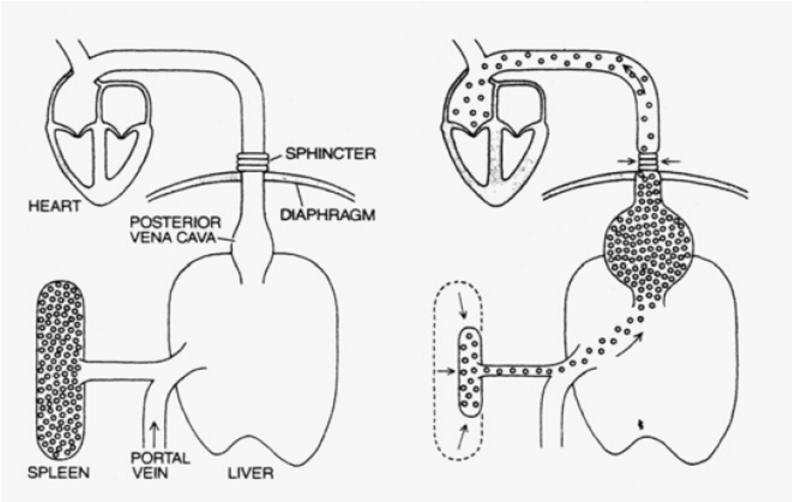
Seal spleen:

- 4.5% of body weight
- correlates with dive depth

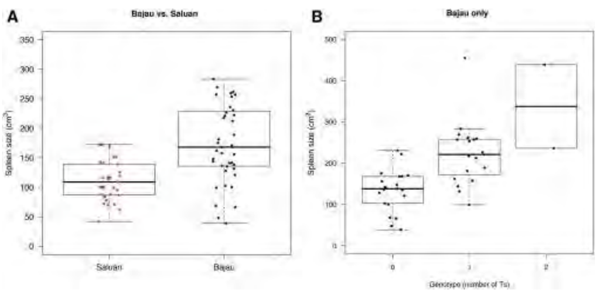


Oxygen and the diving seal. Thornton SJ, Hochachka PW. UHM 2004;31:81-93

Spleen contraction



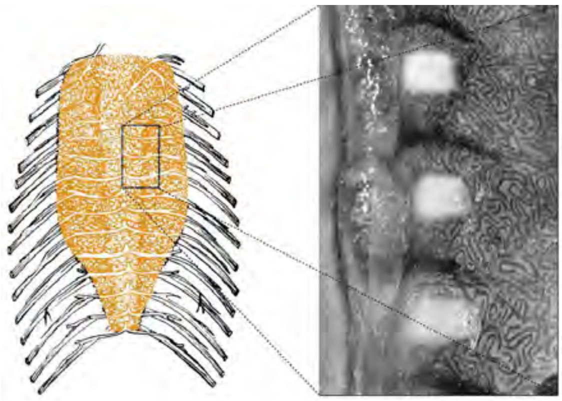
Large spleen Bajau people



genetic adaptation
gene PDE10A

Ilardo M. et al, Physiological and Genetic Adaptations to Diving in Sea Nomads. *Cell 173, 569–580, April 19, 2018*

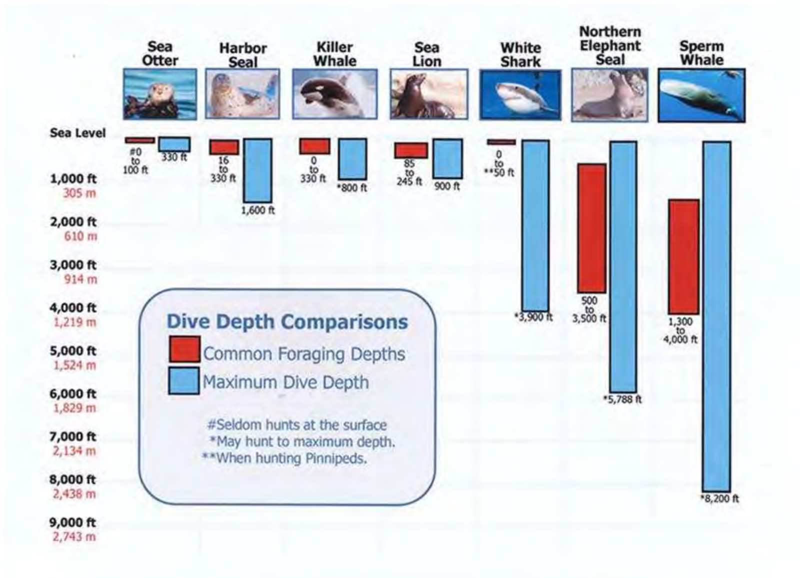
Retia mirabilia



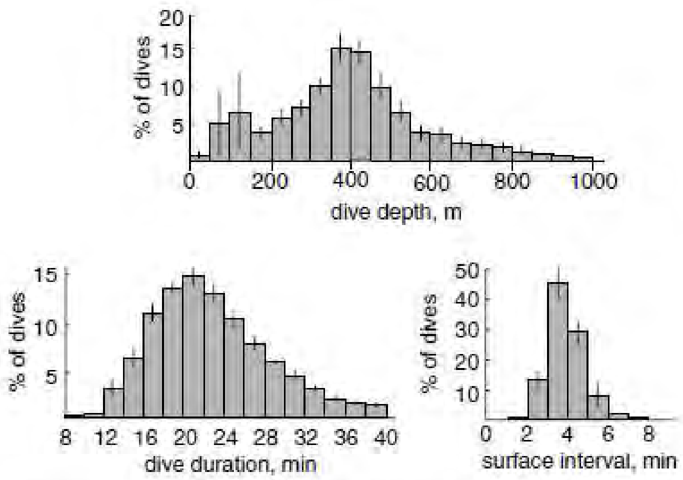
- contorted spirals of blood vessels, arterial + veneus
- blood reservoir (oxygen storage)
- to accommodate increased thoracic blood volume (peripheral blood shift)

Pfeiffer, C. J., and T. P. Kinkead (1990). "Microanatomy of Retia Mirabilia of Bowhead Whale Foramen Magnum and Mandibular Foramen."Acta Anat. 139: 141–150.

Dive patterns

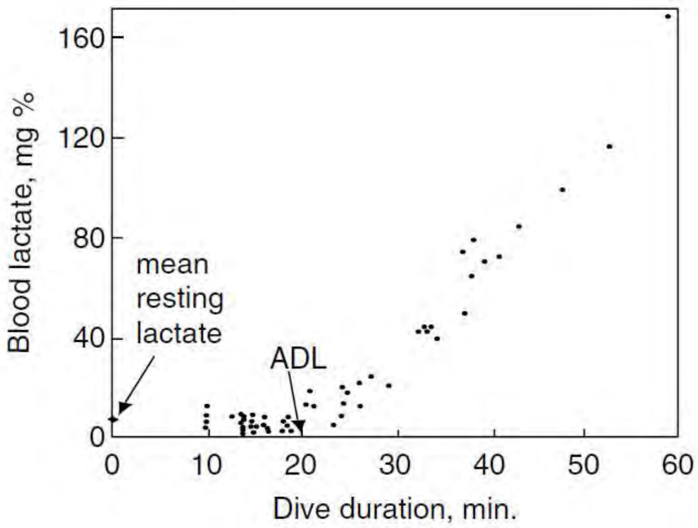


Dive patterns



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)



Kooyman et al 1981

Commercial apnea divers

- commercial skin divers (repetitive within ADL)
  - Ama divers (Japan and Korea) average dive time: 38 sec with equal surface intervals, foraging at 5-12 msw

Shallow vs deep

<u>Shallow divers + terrestrial</u>

- sea otter, fur seal, human
- inspiration before diving
- O_2 source storage = lung
- dive within ADL

<u>Deep divers</u>

- weddell seal, whales
- seals exhale before diving
- O_2 storage = Hb & myoglobine
- most dives < ADL
- can go beyond ADL

Snyder GK. Respiratory adaptations in diving mammals. Resp Physiol. 1983;54:269-294

N. Elephant seal

- 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

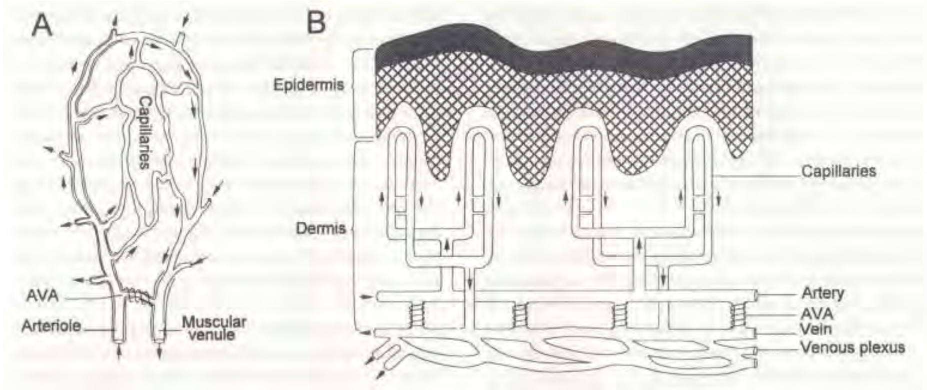
<u>centralization</u>

- brain
- retina
- lung
- heart

<u>peripheral shutdown</u>

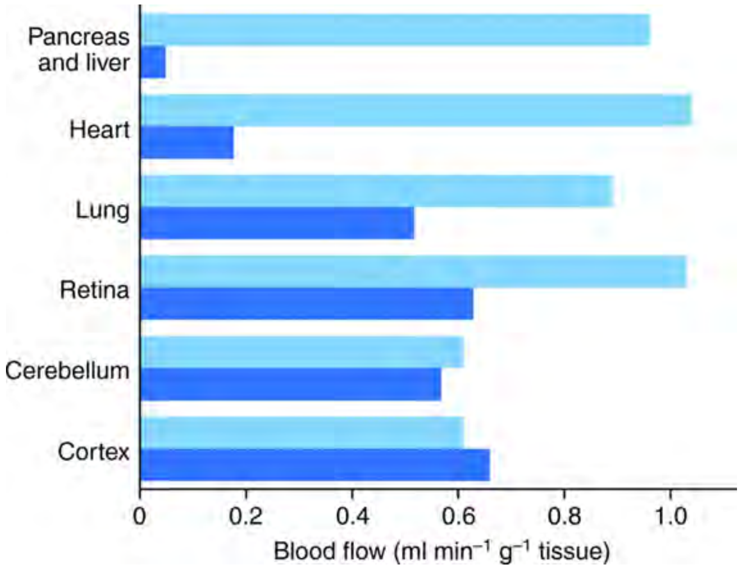
- skin
- muscle
- splanchnic organs

AV anastomosis



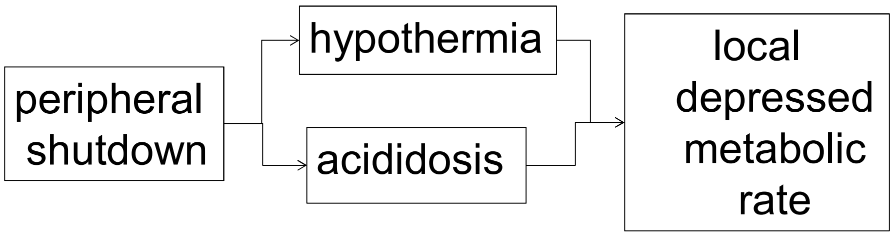
Kooyman GL. Diverse divers: physiology and behavior. 1989 Springer-Verlag, Berlin

Redistribution Weddell seal



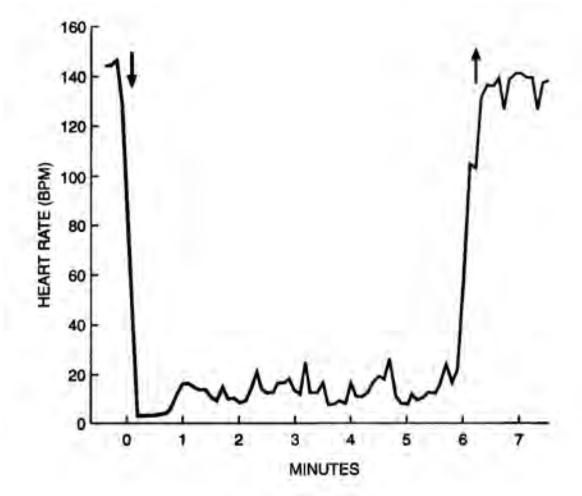
Zapol WM, Liggins GC, Schneider RC, et al. Regional blood flow during simulated diving in the conscious Weddell seal. JAP 1979;47:968-973

Metabolic depression

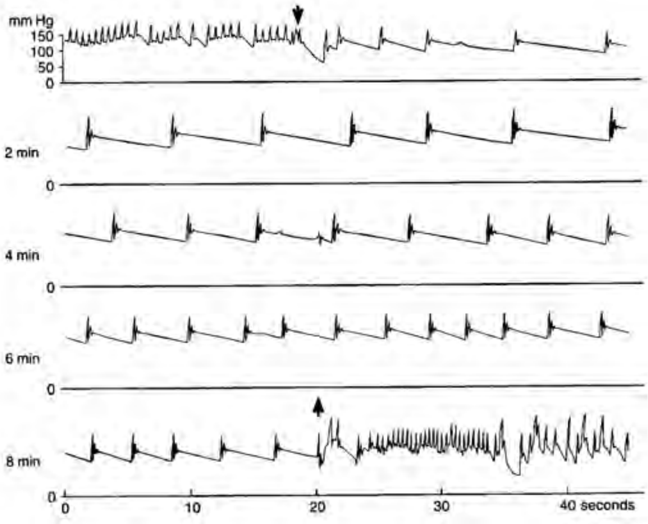


Core temperature is maintained!

Bradycardia (seal)



Maintained MAP

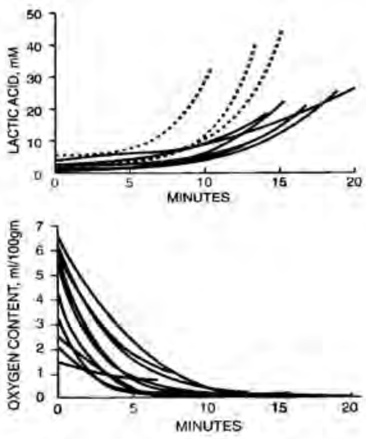


Aortic bulb

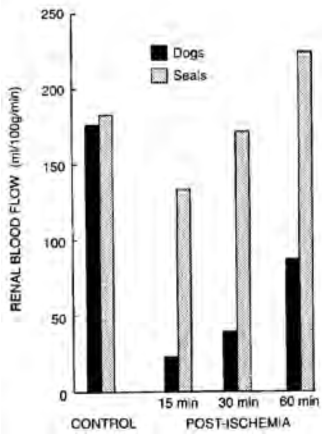
- heart frequency down to 5%
- increased stroke volume
- aortic bulb & elastic recoil
- windkessel function

Ventral view of heart of Weddell seal

Ischemic tolerance



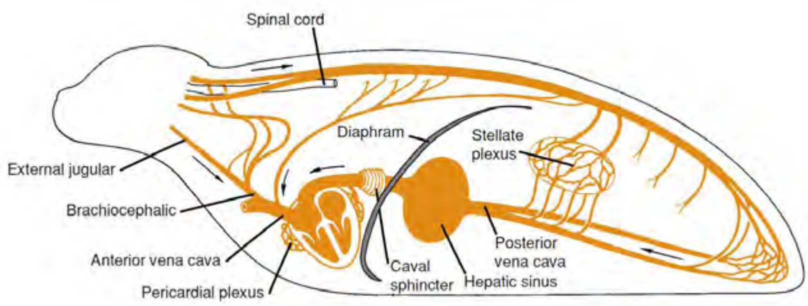
accumulation of muscle lactate and oxygen depletion in harbor seals



renal blood flow before and after 60 min of ischemia

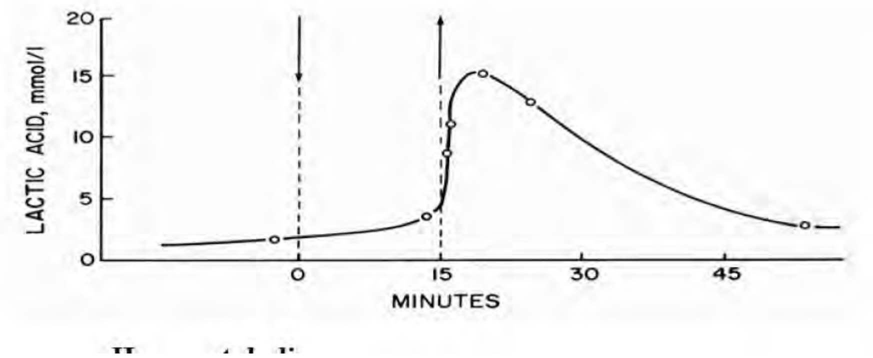
Halasz NA, Elsner R, Garvie RS, et al. Renal recovery from ischemia: a comparative study Of seal and dog kidneys. Am. J. Physiol. 1974;227:1331-1335

Caval spincter



- only in seals!
- to prevent venous return
- to titrate autotransfusion (spleen)
- to protect the heart against acidotic blood

O_2 debt



Grey seal, experimental dive in captivity

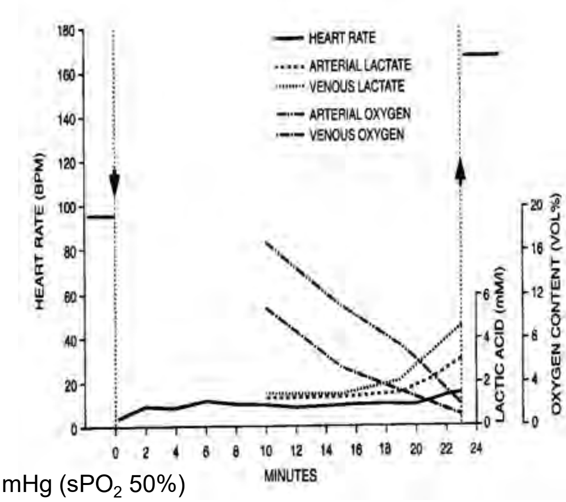
Blood gasses

Weddell seal	***duration***	***PO_2***	***PCO_2***	***pH***
Free dive	*27 min*	*18 mmHg*	*55 mmHg*	*7.3*
Forced submersion	*55 min*	*10 mmHg*	*84 mmHg*	*7.11*

Weddell seal	***duration***	***PCO_2***	***pH***	***lactate***
forced submersion	*61 min*	*post dive 55 mmHg*	*post dive 6.8*	*max 26 mmol/L*
free dive	*< ADL*			*max 2 mmol/L*

Cerebral hypoxic tolerance

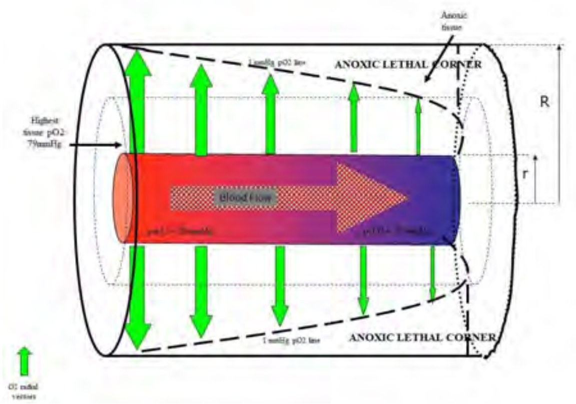
- hypoxic tolerance down to PaO_2 8 mmHg in Harbour seal
- enhanced anaerobic capacity!
- high brain capillary density
- neuroglobin

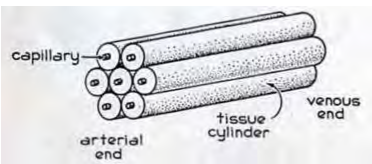


(Humans unconscious: PO_2 < 30 mmHg (sPO_2 50%))

Burmester T and Hankelen T. What is the function of neuroglobin? J Exp Biol 2009;212:1423-1428
Kerem D, Elsner R. Cerebral tolerance to asphyxial hypoxia in the harbour seal. Respiration physiology 1973;19:188-200

Krogh cylinders



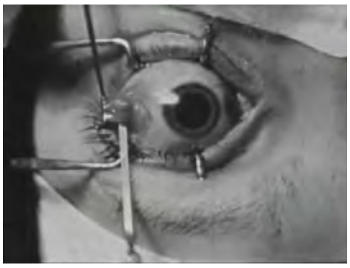


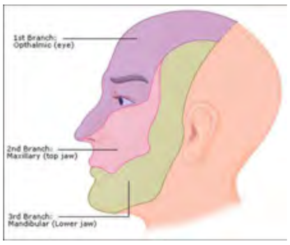
Capillary 30-60 μm from tissue cell

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

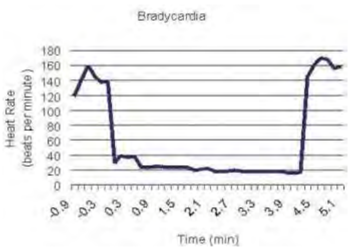
- hypoxia, hypercapnia and acidosis reinforce dive response
- pulmonary inflation (ascend) terminates dive response
- conscious control!
  - variable bradycardia
  - modest dive response if voluntary shallow dive within ADL

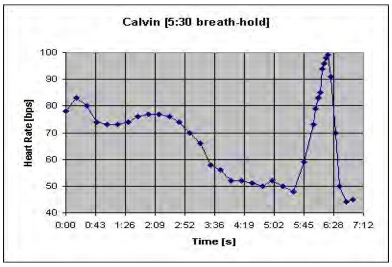
Other species

- all vertebrates exhibit a dive response.
- caiman from 28 > 2 beats/min.
- neural pathways are universal
  - sympathetic > vasoconstriction
  - parasympathetic > bradycardia

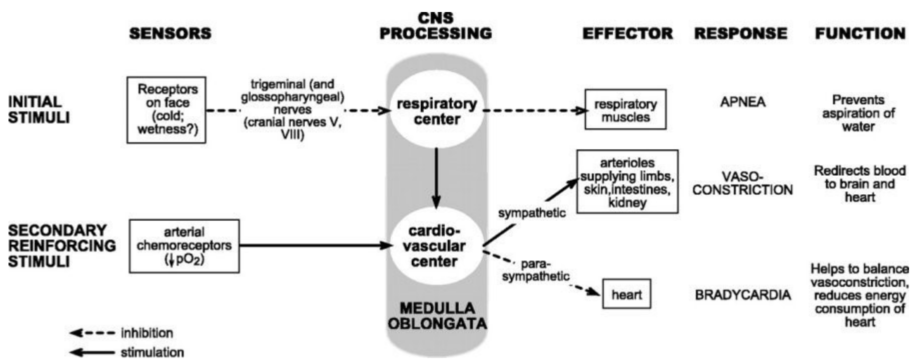
Schreer JF. Allometry of diving capacity in air-breathing vertebrates. Can J Zool 1997;75:339-358

Bradycardia in free divers





Dive resonse wiring



Summary

- most dives within ADL
  - greatly enhanced O_2 stores
- dive response
  - centralisation of circulation
  - bradycardia
  - anaerobic
- many adaptations

Thank you for your attention!

Slides available at www.mattijnb.nl

contact: mattijnb@gmail.com