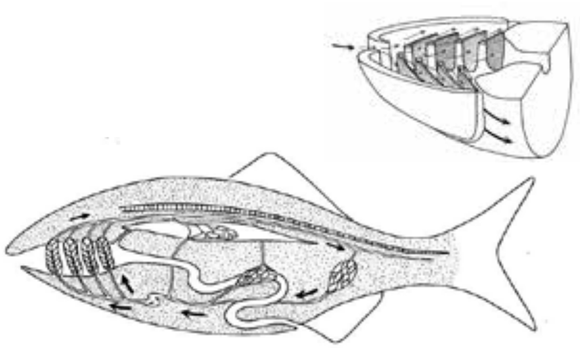
I. Swimbladder & Buoyancy

II. Circulation & Respiration



I. Swimbladder (gas bladder) and buoyancy:

- regulating buoyancy allows control of depth in water without using muscles to fight gravity (saves energy)
- depth regulation helps with vertical stratification of:
  - **food**
  - **predators**
  - **temperature**
  - **light**
  - **oxygen**

Buoyancy:

- basic problem: if more dense than water, a body sinks, if less dense, it floats
  - specific gravity of water: **fresh = 1.0, marine = 1.026**
  - fish sink: bony fish specific gravity = **1.06 - 1.09**

bone & scales = 2.0
cartilage = 1.20
muscle = 1.05 - 1.10
lipids = 0.90 - 0.93

Many ways to stay afloat:

1. **generate lift** (active)
   - generate **lift** with pectoral fins
2. **reduce density** (static)
   - reduce mass of heavy tissues (skeletal and muscle tissue)
   - lipids
   - swimbladder ...

Generate Lift (active)

- pectoral fins of sharks and scombrids act like wings of airplanes

- some fish hover by “flapping” their pectoral fins (e.g. hovering gobies)

Generate Lift (active)

Advantage: can move freely up and down in water column

Disadvantages:
- high energy expenditure
- must maintain certain speed of movement

Works best for:
- **i) cruising specialists**
- **ii) bottom dwellers**

Reduce Density (static)

1. **Reduce amount of dense materials**

How?
- reduced calcification of bones
- reduction of protein in muscles
- increase in water

Who?
- deep sea (meso and bathypelagic) fishes

Advantage: buoyancy doesn’t vary with depth

Disadvantage: restricts swimming ability

Reduce Density (static)

2. Storage of Lipids

Types:
- squalene (shark livers)
- wax esters (coelacanth)
- lipids (oilfish)

Advantage: buoyancy doesn’t vary with depth

Disadvantage:
- fine-tuning is difficult
- buoyancy regulation linked to metabolism

Reduce Density (static)

3. Swimbladder (= gas bladder, airbladder)

Definition = gas filled sac above gut & below vertebral column
- develops from outpocket of esophagus (originally used as lungs?)
- only found in bony fishes

Advantages:
- gas is light
- precise control possible
- no relationship to energy storage
- energetically inexpensive
- many strategies possible: sit & wait, slow cruising, hovering
- other uses: sound producer/detector

Disadvantage:
- large depth changes not practical over short time period

Why?

Boyle’s Law:

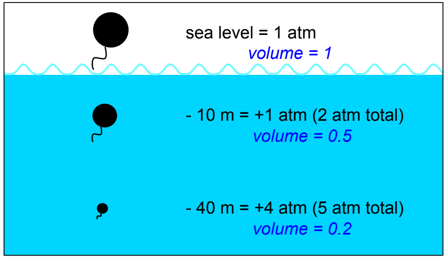
http://www.mbayaq.org/video/video_popup_dsc_pressure.asp

At a constant temperature, volume of a gas varies inversely with absolute pressure:

$$P_1V_1 = P_2V_2$$

P = pressure
V = volume

- Pressure increases 1 atmosphere for every 10 m in depth



sea level = 1 atm
volume = 1

- 10 m = +1 atm (2 atm total)
volume = 0.5

- 40 m = +4 atm (5 atm total)
volume = 0.2

Thus, a fixed amount of gas will provide less buoyancy at greater depths

- e.g., a fish descending from the surface to 10 m has the volume of its swimbladder halved
- how do fishes solve this problem?

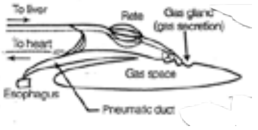
Add or Remove Gas

How?

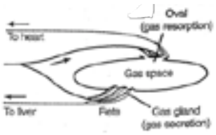
Depends on type of swimbladder ...

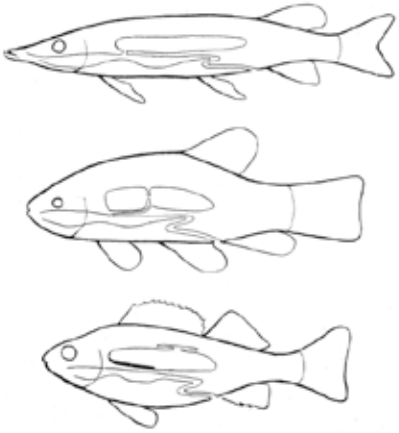
Swimbladder: two types

Physostomous — connected to esophagus via pneumatic duct (ancestral: soft-rayed fishes only, salmonids, minnows, herrings, etc.)



Physoclistous — not connected to gut (derived)





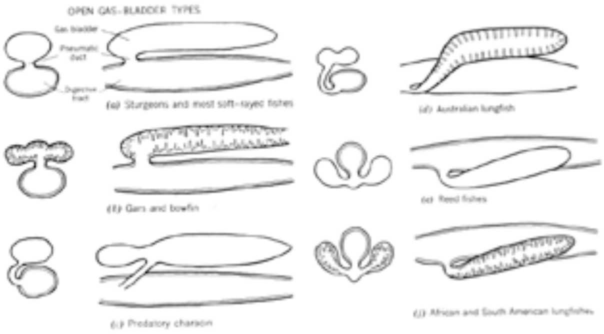
Physostomous

Physostomous

Physoclistous

Types of Physostomous Swimbladders/Lungs

- swimbladder: dorsal duct off esophagus
- lungs: ventral duct off esophagus



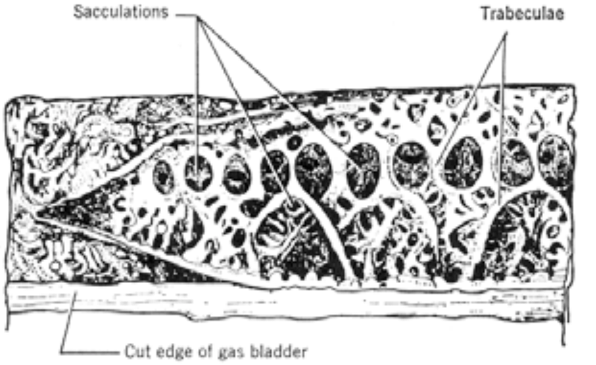


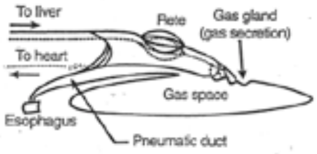
Fig. 8.11 Sacculation as shown in a portion of the wall of the gas bladder in an African lungfish (*Protopterus*). (Based on Spencer in Bronn, 1940).

Physostome solution:

- add gas by gulping air or secreting gas into bladder (gas gland & rete mirabile)
- remove gas by burping (pneumatic duct)

Disadvantage: fish can be dependent on surface

- aerial predation risk higher
- problematic for fish diving to depths -- deeper means more air necessary to provide buoyancy, but more air makes it more difficult for fish to descend in the first place

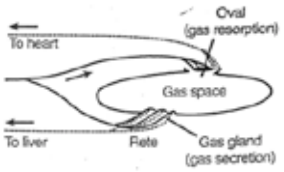


Physoclistous solution:

- add gas by secreting gas into bladder (gas gland & rete mirabile)
- remove gas by resorption via oval vascular patch

A. Secretion (gas gland & rete)

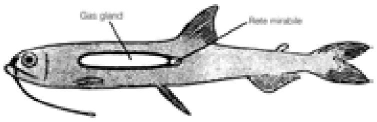
B. Resorption (oval)



Secretion into swimbladder (gas gland & rete mirabile)

(used by physoclists & many physostomes)

- gases added by diffusion from blood into swimbladder at specialized region known as the gas gland (glandular patch with rich blood supply)
- problem: need higher partial pressures / concentration of gases in blood than in swimbladder
  - — how can this happen given high pressures in swimbladder?



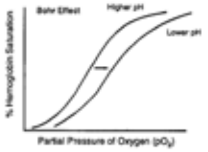
Secretion into swimbladder (gas gland & rete mirabile)

Keys to gas secretion into swimbladder:

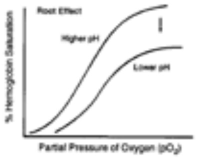
- Bohr effect
- Root effect
- Salting out
- Rete Mirabile & Countercurrent exchange

Acidification of blood releases O_2 from hemoglobin

Bohr Effect: as blood pH falls, pO_2 required to saturate hemoglobin with O_2 increases, and O_2 is released, increasing pO_2 in blood



Root Effect: as blood pH falls, hemoglobin cannot become completely saturated with O_2, and O_2 is released, increasing pO_2 in blood



Salting Out: lactate and hydrogen ions produced by the gas gland (via anaerobic metabolism) reduce solubility of gases in aqueous solution, thereby easing transport into gas bladder

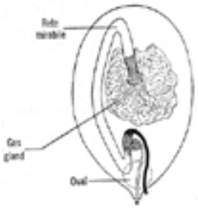
- combined effects of Bohr Effect, Root Effect, and Salting Out could fill a gas bladder down to about 25 m. Below that, gas would simply stay in solution in blood.
- but fish caught from depth of 7000 meters have full gas bladders, with pressures inside the bladder in excess of 700 atm….

Rete Mirabile and Countercurrent Exchange

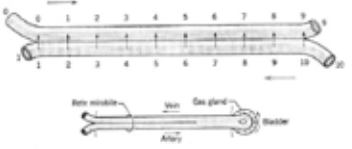
Rete Mirabile and Countercurrent Exchange

Rete Mirabile: composed of many small, tightly packed, looped capillaries. Leads to gas gland.

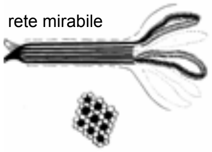
In rete, partial pressures (concentrations) of gases are elevated by countercurrent exchange



countercurrent exchange of gases

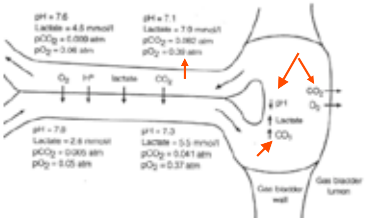


rete mirabile



Rete Mirabile and Countercurrent Exchange

1) tissues of gas gland respire anaerobically (even when O_2 present), producing lactate and hydrogen ions (*decreasing pH*)
2) gas gland cells produce CO_2 from bicarbonate, some of which combines with H_2O to produce carbonic acid -- *further lowers pH*. High levels of CO_2 in blood also cause direct addition into bladder.
3) *drop in pH* triggers Bohr and Root effects in the gas gland -- causing hemoglobin to release O_2, increasing O_2 concentrations in the blood
4) these effects are *amplified* because O_2, H+, lactate, and CO_2 diffuse down partial pressure gradients along the rete



other considerations:

1) the longer the rete, the greater the pressure that can be achieved.

   -- a rete 1 cm long can continue to secrete O_2 into a gas bladder up to a partial pressure of 2000 atm
   (corresponding to a depth of 20,000 meters!)

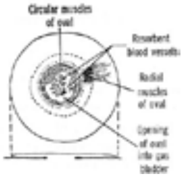
2) secretion takes time

   -- fish whose gas bladders are emptied take between 4 and 48 hours to refill

Resorption (removal of gases from swimbladder via blood)

- most of the wall of the swim bladder is not gas permeable because:
  - poorly vascularized
  - lined with sheets of guanine crystals

- gas resorbed at modified area called **oval**
  - gas diffuses at oval
  - carried by blood to gills
  - controlled by:



1. controlling flow of blood to resorptive area
2. using muscular sphincter to control gas flow to resorptive area

Conditions for reduction or absence of swimbladder

1) bottom dwelling or in swift streams (e.g., gobies, sculpins)

2) continuous swimming over wide depth range (some tunas)

3) vertical migrators – an organ with fat and/or increase lipid content of body

4) bathypelagial inhabitants - sparse food (>1000m): expensive to have gas bladder – reduce tissues to near neutral buoyancy

- only about 50% of bony fishes have swimbladders (convergent evolution in many groups)

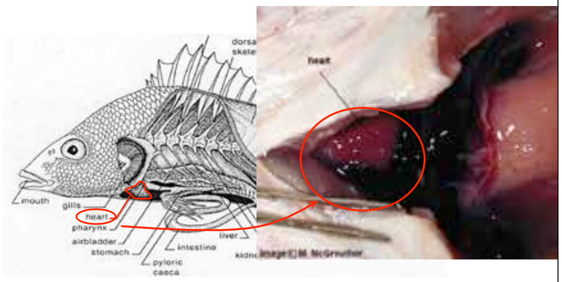
II. Circulation and Respiration

Circulation (heart & vessels)

1. Heart

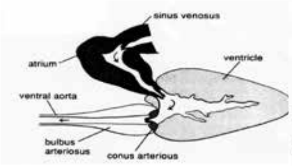
- simple, two chambered heart in most fishes

(hagfish possess multiple “accessory” hearts)

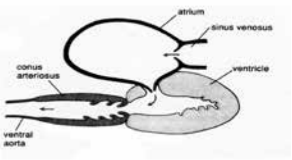


1. Heart

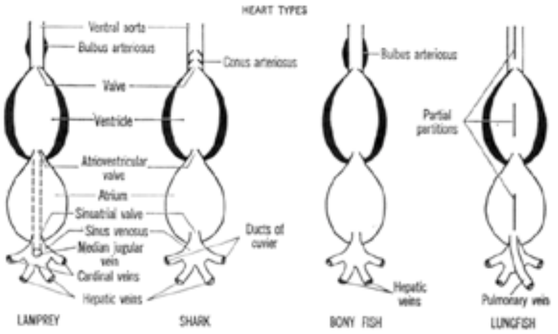
- sinus venosus (collects blood from liver & ducts of Cuvier)
- atrium (1st chamber: initial acceleration of blood flow)
- ventricle (2nd chamber: main propulsive force for cardiac flow)
- bulbous arteriosus (bony fish) or conus arteriosus (lampreys, hagfish, elasmobranchs & a few primitive bony fishes, e.g. gars) (smooths flow of blood to gills)



Bony fish

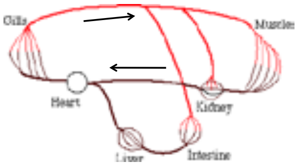


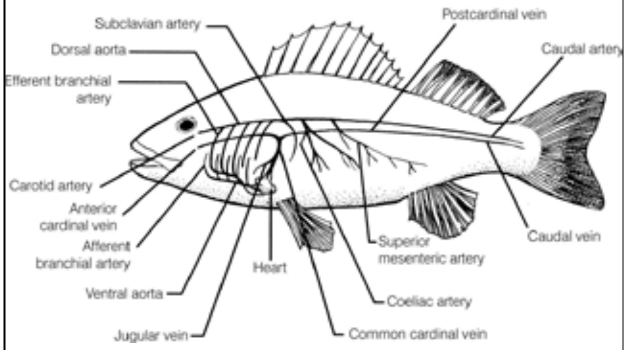
Shark



2. Circulatory system

- direction of blood flow
  - blood is carried from the heart to the gills via the ventral aorta into afferent branchial arteries
  - oxygenated blood flows from the gills via the efferent branchial arteries into the dorsal aorta (in the hemal canal) and is carried to the head and body via numerous arteries
  - blood returns via numerous veins, many of which empty into the hepatic portal system (liver) and return to the heart via cardinal veins and then into the sinus venosus





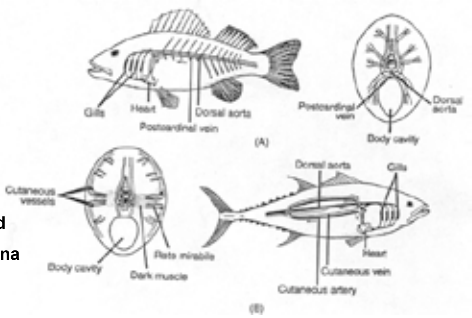
Remember, warm blooded fishes do it differently (scombrids & lamnids):

- cool blood from gills passes along the cutaneous artery
- then into muscle mass through a rete mirable that allows conservation of heat generated by the swimming muscles

A. "Typical" fish

B. Warm-blooded

e.g, bluefin tuna



Respiration (gills & blood)

I. Challenges of breathing in water

II. Blood

III. Gills

Challenge

– extract O_2 from water and distribute it to the cells in the body, fast enough to meet metabolic demands and prevent lactic acid buildup

Difficult because: 1. **Concentration of oxygen is low in water**

$[O_2]$ air is approximately 21% by volume

$[O_2]$ water <1% by volume

2. **Water is dense and viscous**

- H_2O is 800x more dense than air
- H_2O is 50x more viscous

- **Therefore, more energy is required just to move water across respiratory surfaces**

(fishes use about 10% of the O_2 extracted from water just to keep breathing muscles going -- we use 1-2%)

Additional considerations:

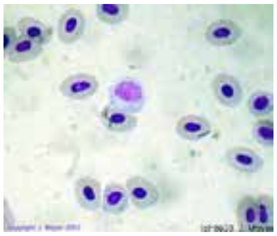
Solubility

- solubility decreases as temperature increases
- solubility decreases as salts / solutes increase

thus, warm water has less O_2 than cold water, and salt water has less O_2 than freshwater

Blood

- red and white blood cells
- produced by spleen & kidney (instead of bone marrow)
- red blood cells are nucleated




Blood

- most fish have hemoglobin (respiratory protein) to increase O_2 carrying capacity of blood, but...
  - -- Antarctic fish don't (also have anti-freeze in blood)
  - -- most larval fish don't (unpigmented for camouflage?)

- hemoglobin concentration correlated with lifestyle and environment
- varies seasonally


Blood

— hemoglobin binding of O_2 is affected by ....

temperature – higher temperatures lower affinity for O_2

pH, CO_2 levels } low pH, lower affinity for O_2 (high CO_2 ⇒ low pH)

- Bohr Effect
- Root Effect (only some species)

- hemoglobin has high affinity for O_2 at gills and low affinity for O_2 in muscle tissues (low pH & warmer)
- thus, O_2 is strongly bound by hemoglobin at gills & dumped at muscle tissues & diffuses from blood into them

Gill structure and Gas Exchange (water ⇔ blood)

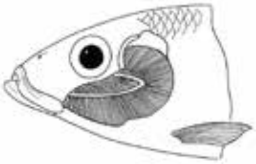
Gills

— main site of gas exchange, but others are used…

- skin (larvae)
- roof of mouth (e.g., electric eel)
- gut (e.g., *Plecostomus*)
- lungs / swimbladders (e.g., lungfish / gars)

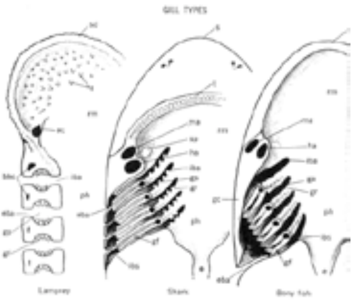
— other uses of gills…

- osmotic regulation
- disposal of metabolic waste (e.g., ammonia)
- filter feeding with rakers (original use)



Evolutionary trends:

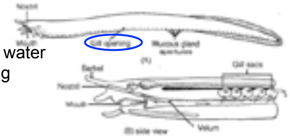
1. **Agnathans** - pouch gills
2. **Elasmobranchs** - gills lay on septa that become external valves - separate gill slits
3. **Bony fishes** - gills on short internal septa, single opening (opercular opening)



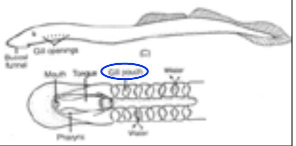
Evolutionary trends:

Agnatha: - intake through nostril **(hagfishes)**
- ventilation pump = **velum**
- 1 - 16 **gill sacs**

- when hagfish head is buried in prey, water comes in and out through gill opening behind last gill pouch



- **lampreys** expand and contract the gill pouches, cause water to flow in/out: practical when head buried in prey

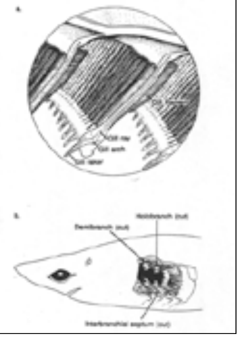


Elasmobranchs: (evolutionary trends continued…)

- intake through mouth and **spiracle**
- ventilation either **ram** (mouth) or **pump** (mouth & spiracle)
- ≥ 5 individual external **gill slits** (vs. single operculum)

structure:

- **gill arch** and **gill ray** (support gill filaments)
- **gill rakers** (protect filaments and collect food)



Teleosts: (evolutionary trends continued…)

- intake through mouth
- ventilation either **ram** (scombrids - obligate) and/or **pump**

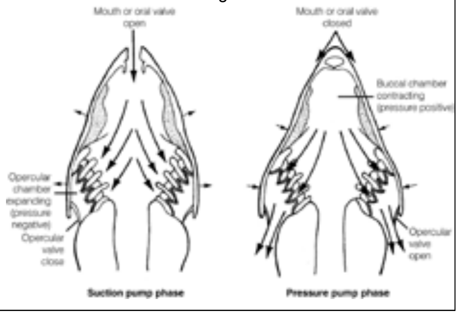
pumping (most fish)

or

ram ventilation (e.g., tunas & mackerels, some sharks)

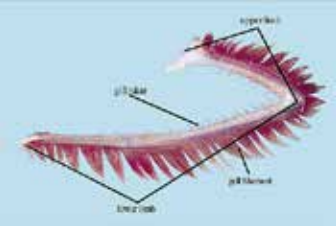
Double pump system

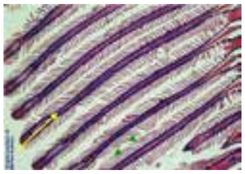
1. buccal (B) pump
2. opercular (O) pump
    - expand and contract the cavities with valves to prevent back flushing (labial flaps, opercular flaps)
    - provide almost continuous flow over gills



Gill structure (Teleosts):

- 4 **gill arches** with **rakers**
- pairs of **gill filaments**
- **secondary lamellae** (sheet-like folds)
- **countercurrent exchange**





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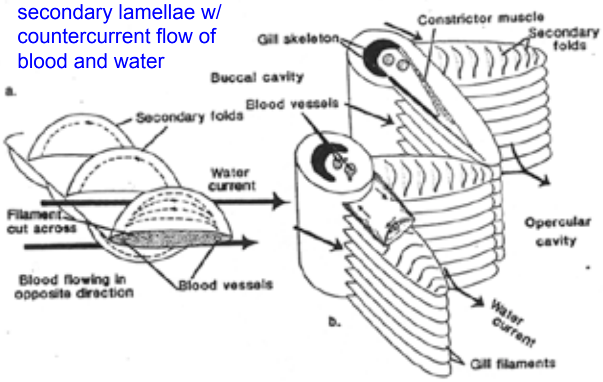
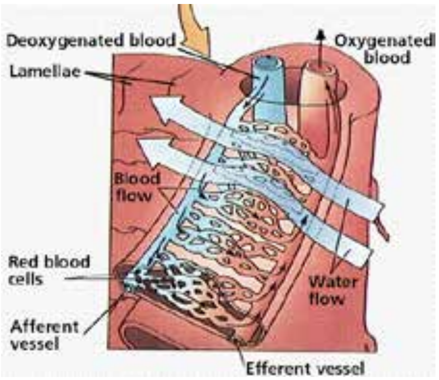
gill filaments (paired)

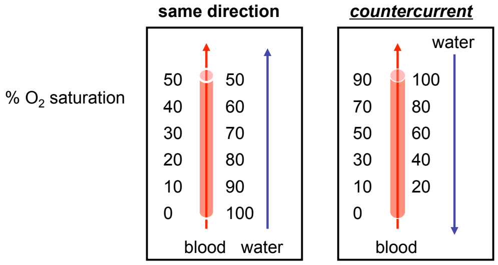
secondary lamellae w/ countercurrent flow of blood and water





Countercurrent exchange

- allows efficient extraction of O_2 — up to 80% removed (vs. 20% by humans)



same direction

countercurrent

% O_2 saturation

Gill morphology is related to activity levels

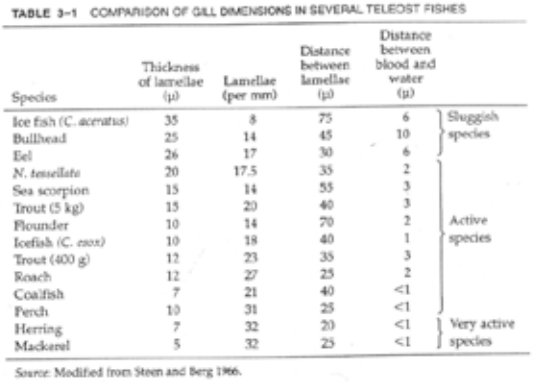


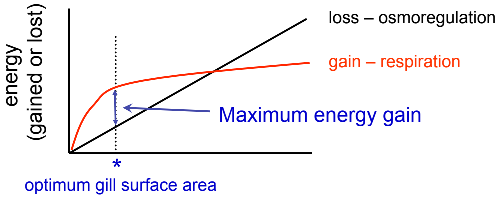
TABLE 3–1 COMPARISON OF GILL DIMENSIONS IN SEVERAL TELEOST FISHES

Species	Thickness of lamellae (µ)	Lamellae (per mm)	Distance between lamellae (µ)	Distance between blood and water (µ)	
Ice fish (*C. aceratus*)	35	8	75	6	Sluggish species
Bullhead	25	14	45	10	
Eel	26	17	30	6	
N. tessellata	20	17.5	35	2	Active species
Sea scorpion	15	14	55	3	
Trout (5 kg)	15	20	40	3	
Flounder	10	14	70	2	
Icefish (*C. esox*)	10	18	40	1	
Trout (400 g)	12	23	35	3	
Roach	12	27	25	2	
Coalfish	7	21	40	<1	
Perch	10	31	25	<1	
Herring	7	32	20	<1	Very active species
Mackerel	5	32	25	<1	

Source: Modified from Steen and Berg 1966.

Optimal gill size is determined by tradeoff between...

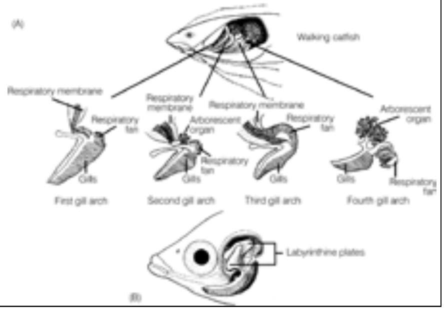
- energy gains from respiration
- energy losses from osmoregulation



gill surface area

Other organs used to respire:

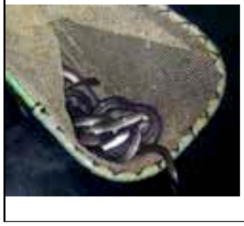
- skin
- lungs
- gut
- roof of mouth
- specialized structures in branchial cavity (e.g., arborescent organs)



Cutaneous (skin) Respiration

- e.g., freshwater eels
- larvae of many species whose adults are regular gill breathers

-- cutaneous surfaces account for 96% of respiratory surface in larval chinook salmon



Newly hatched salmon with yolk sac.

<u>Air-breathing fishes</u>:
most live in tropical freshwater habitats: So. America, Africa, Asia, 40 genera, 13 orders

Use a variety of organs:

a. modified gills (thick lamellae) - e.g., walking catfish
   - necessary because regular gills stick together out of water

b. mouth (vascularized buccal cavity) – e.g., electric eel has degenerate gills (will drown if kept under, must surface every minute to replenish oxygen supply)

c. swimbladders & lungs:
   - most swimbladders not well vascularized, some are: e.g., Arapaima, gars, bowfin
   - lungs in lungfish