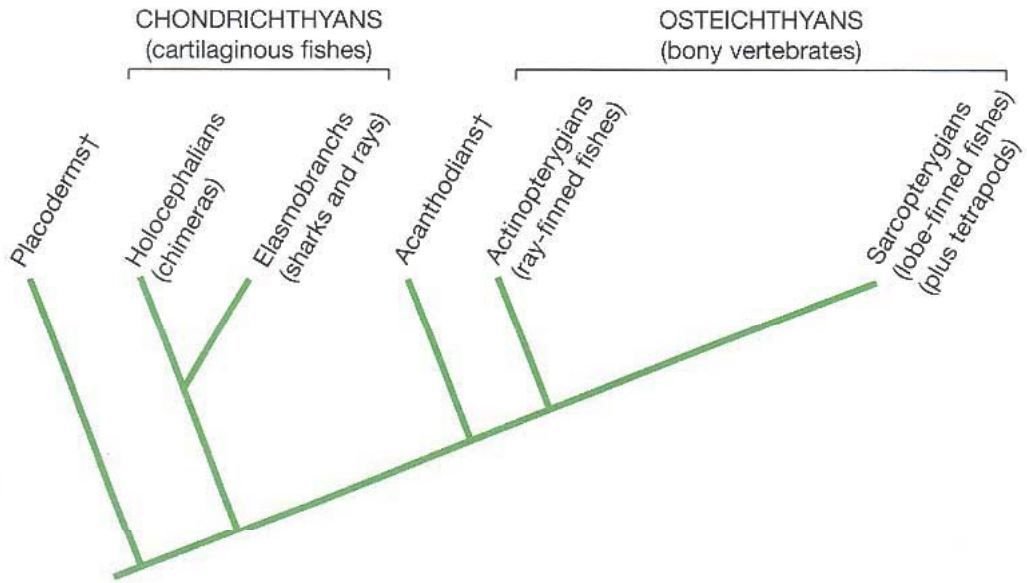
Diversification of Chondrichthyes and adaptations to life in water

Textbook Chapters 4 & 5

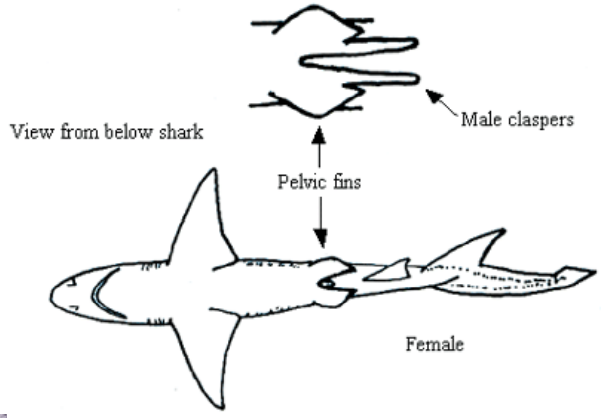
Phylogenetic placement of Chondrichthyans

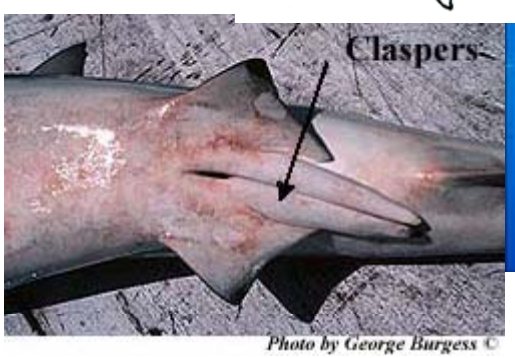
- As we know, Placoderms were jawed fishes sister to Chondrichthyes
  - Note 2 clades of Chondrichthyans
    - Holocephalans: ratfish, rabbitfish, chimera
      - Have one gill opening on each side of head
    - Elasmobranchs: sharks, skates, rays
      - Multiple gill openings on each side of head

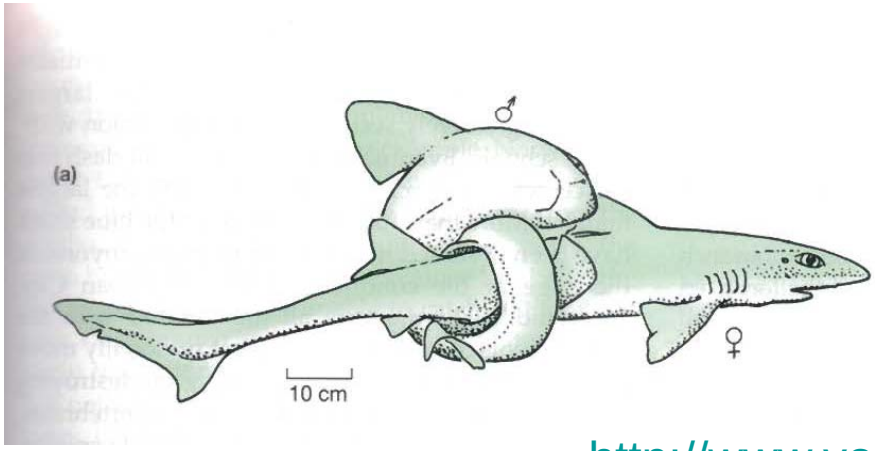


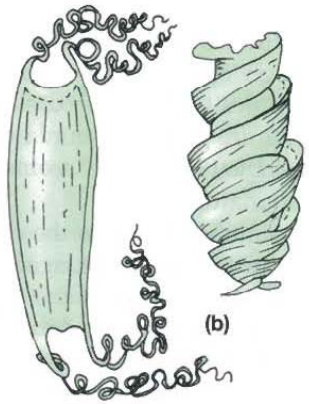
http://www.youtube.com/watch?v=qHnS8_0da6A

- Chondrichthyes diversified in Devonian and have been very diverse ever since
  - Approximately 625 living species.
- Characteristics:
  - 1) Cartilaginous skeleton
  - 2) Second gill arch (hyoid) involved in jaw suspension
  - 3) Males with claspers









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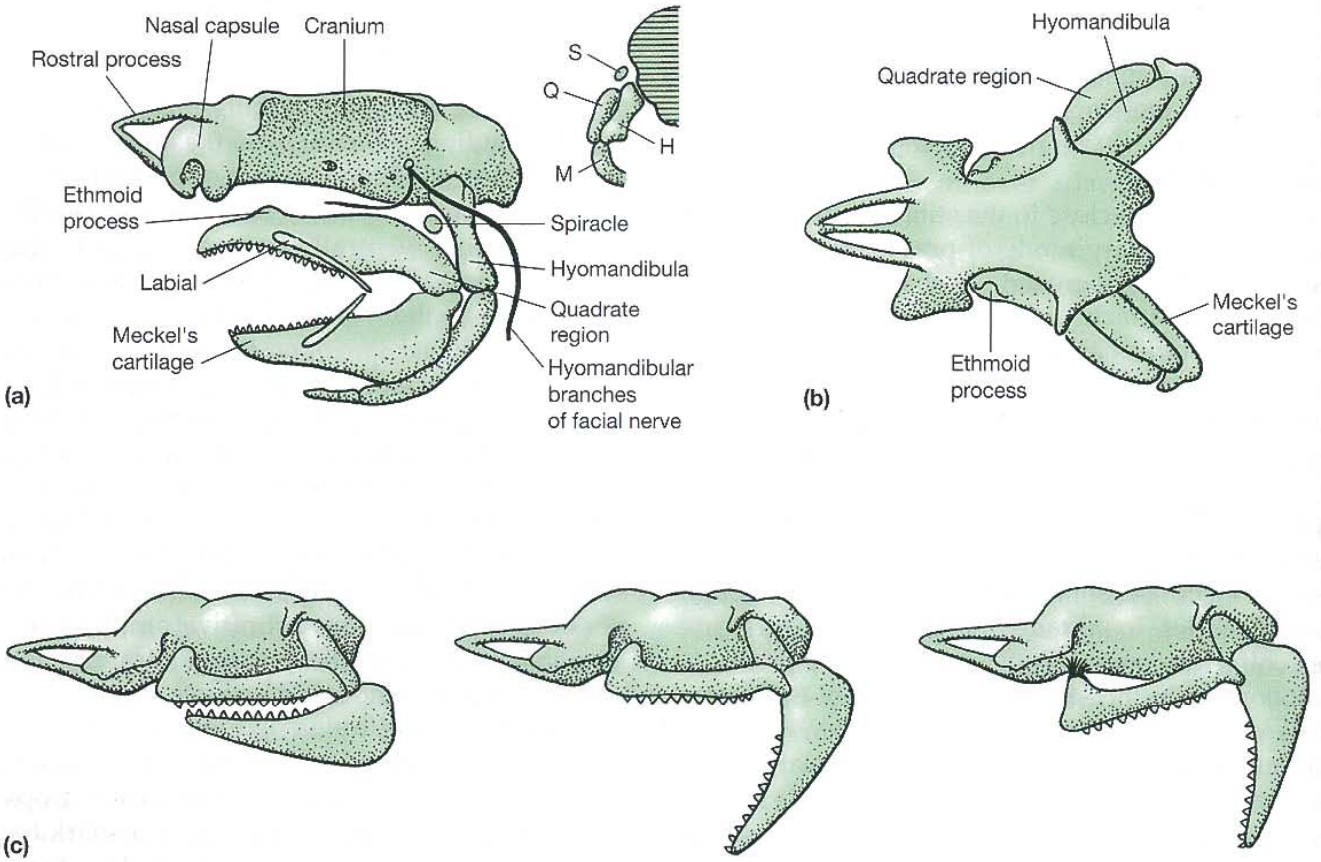
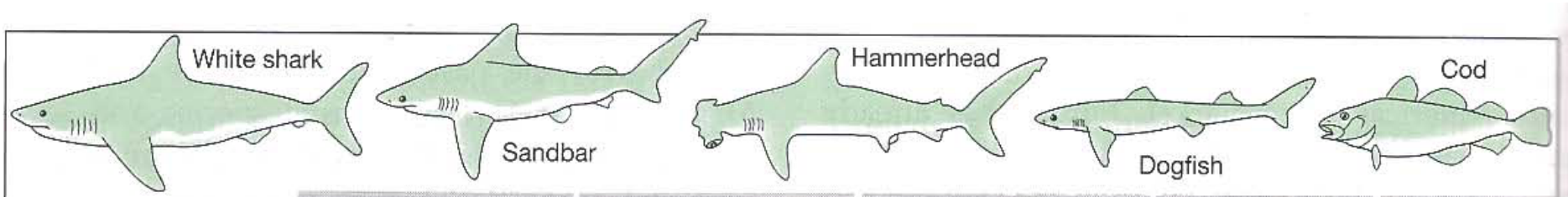
- Jaws: **hyostylic jaw suspension**
  - Hyomandibula braces back of palatoquadrate and attaches to side of cranium (a)
  - Paired palatoquadrate projections (b) attach to chondocranium
- Hyostyly allows for sturdy, moveable jaws, including protrusion of upper jaw (c).



▲ **Figure 5–5** Anatomical relationships of the jaws and chondrocranium of extant hyostylic sharks based on *Scyllium* and *Carcharhinus*. (a) Lateral and cross-sectional views of the head skeleton of *Scyllium* with the jaws closed. S = spiracle; Q = quadrate region of the palatoquadrate; H = hyomandibula; M = mandible. (b) Dorsal view of *Carcharhinus*. (c) During jaw opening and upper jaw protrusion the hyomandibula rotates from a position at a 45° angle to the long axis of the cranium to a 90° angle to that axis.

Study fig 5-7 for the concept, not memorizing the numbers

- Shark life history makes them susceptible to overexploitation:



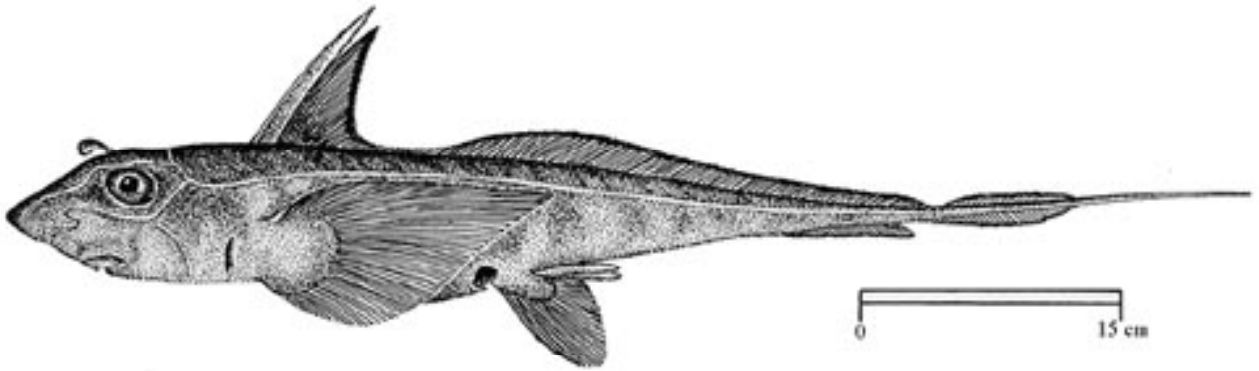
	White shark *Carcharodon carcharias*	**Sandbar** *Carcharhinus plumbeus*	**Scalloped hammerhead** *Sphyrna lewini*	**Spiny dogfish** *Squalus acanthius*	**Atlantic cod** *Gadus morhua*
Age to maturity (years)	m 9–10, f 12–14	m 13–16	m 4–10, f 4–15	m 6–14, f 10–12	m 2–4
Size at maturity (centimeters)	m 350–410, f 400–430	m 170, f >180	m 140–280, f 150–300	m 60, f 70	m 32–41
Life span (years)	m 15(?)	m 25–35	m 35	m 35, f 40–50	m 20+
Litter size	2–10 pups	8–13 pups	12–40 pups	2–14 pups	2 million–11 million eggs
Reproductive frequency	Biennial (?)	Biennial	(?)	Biennial	Annual
Gestation period (months)	>12	9–12	9–12	18–24	n/a

Skates and rays

- More diverse than sharks
  - 456 extant species
- 5-7 gill openings
- 2) Dermal placoid scales usually present
- 3) Spiracle present
- Many benthic rays have sexually dimorphic dentition
  - Males bite females during courtship;
    - Male stingrays' teeth change from blunt teeth like in the females to sharp-cusped teeth during breeding season
  - Females are bigger than males
    - Differences in dentition could be related to diet

- Largest rays, like the largest sharks, are plankton feeders.

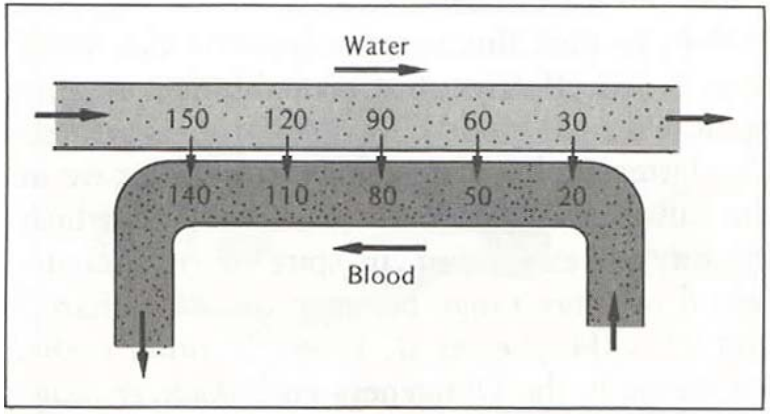
Holocephalians



- 34 species of ratfishes and chimaera
- Many features are shared with Chondrichtyes, but many unique features as well.
- Deep-water marine species (>80 m deep); deposit eggs in shallower water
- Fleshy operculum covers
- Skin naked
- No spiracle
- Flattened, grinding teeth

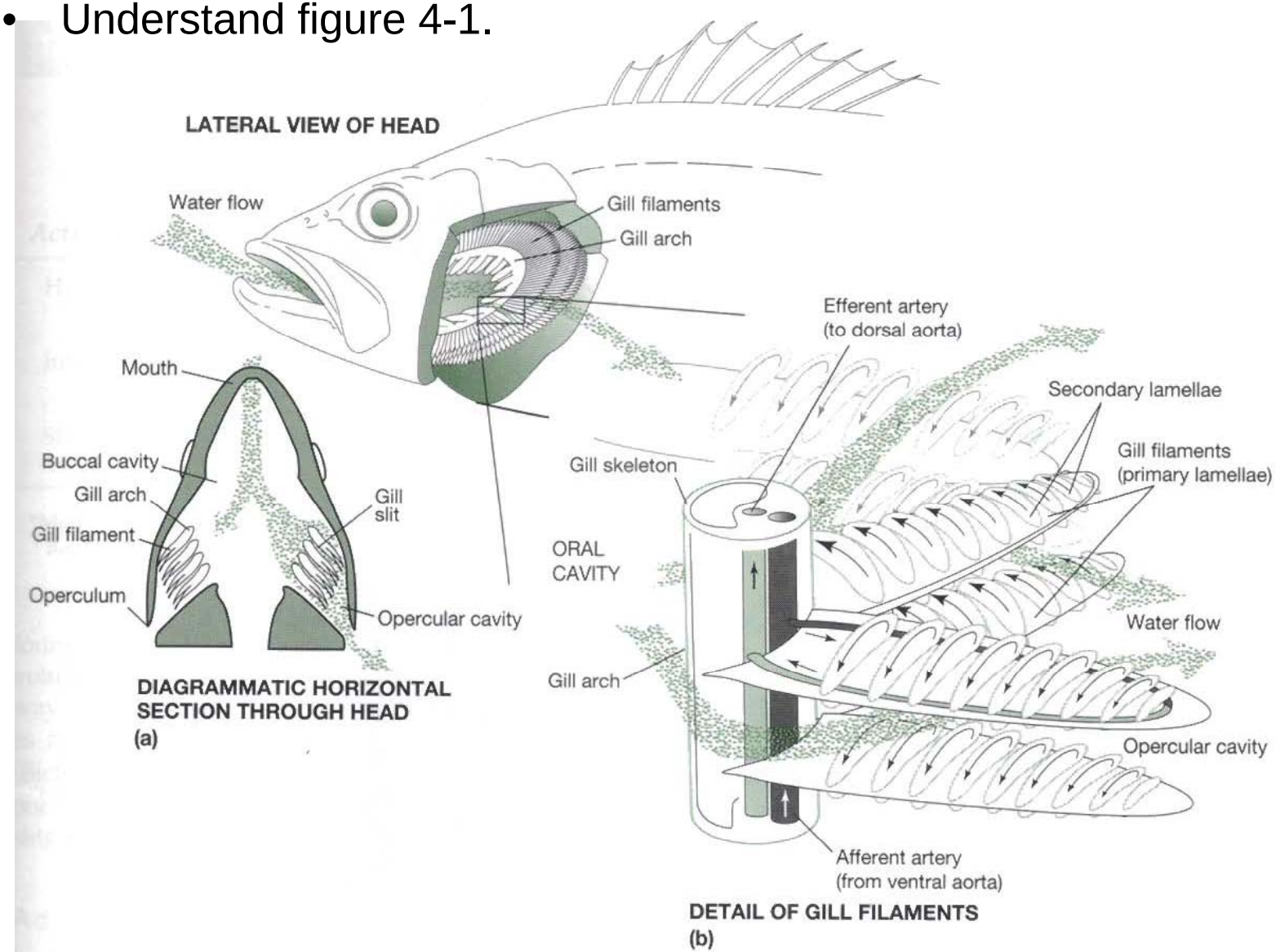
How do gills work?

FIGURE 1.6 Diagram of the countercurrent flow in fish gills. The numbers indicate partial pressures of oxygen (P_{O_2}) in water and blood. The blood enters the gill at a low P_{O_2} (in this example 20 mm Hg), and oxygen diffuses from the water into the blood. As the blood runs along the lamella, it takes up more and more oxygen from the water, and as it leaves the lamella, it has nearly reached the P_{O_2} of the incoming oxygen-rich water. The water, flowing in the opposite direction, gradually loses more and more of its oxygen and leaves the gill after having lost most of its oxygen content.



How gills work

- Understand figure 4-1.



- Operculae prevent backflow into pharyngeal pockets
- Gas exchange takes place at surface of microscopic secondary lamellae
- Mouth and buccal pumping creates flow of water across gills.
  - Recall, that jaws probably evolved to improve filter-feeding and consequently better supply of water across gills.
- Counter-current exchange increases efficiency
  - Blood flows one direction; water the other direction.

Activity, lifestyle, gills are all related

- Refer to table 4.1

TABLE 4.1 The relation among general level of activity, rate of oxygen consumption, respiratory structures, and blood characteristics in fishes of three activity levels

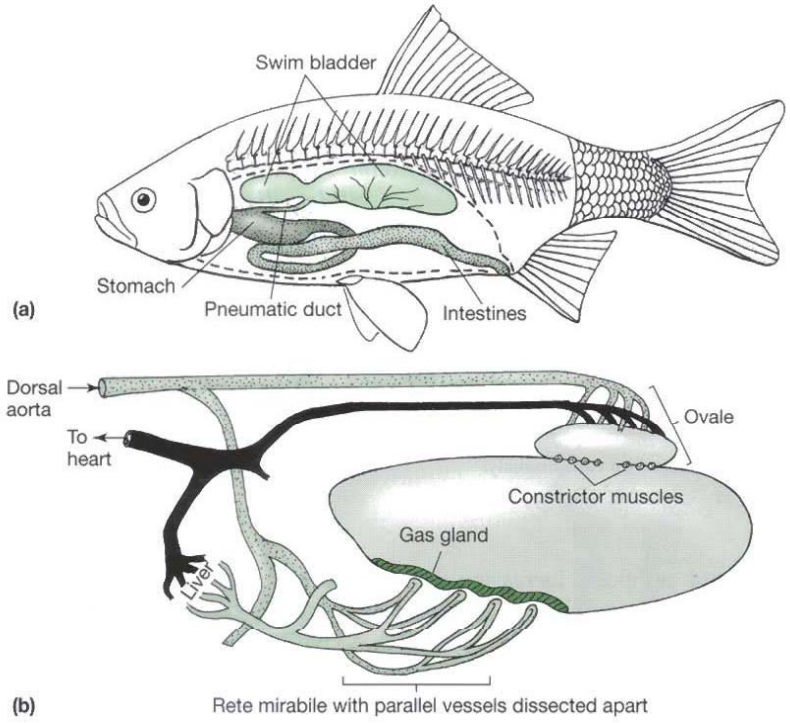
Activity Level	*Species of Fish*	*Oxygen Consumption (mL O_2/g h^{-1})*	*No, Secondary Gill Lamellae (mm^{-1} of primary gill lamella)*	*Gill Area (mm^2/gm body mass)*	*Oxygen Capacity (ml O_2/100 mL blood)*
High	Mackerel* (*Scomber*)	0.73	31	1160	14.8
Intermediate	Porgy (*Stenotomus*)	0.17	26	506	7.3
Sluggish	Toadfish+ (*Opsanus*)	0.11	11	197	6.2

*Modified carangiform swimmers; swim continuously.
+Benthic fish.

Swim bladders

- Two kinds:
  - **Physostomous**: bladder retains ancestral condition where the pneumatic duct connects to gut;
  - **Physoclistous**: bladder does not have connection to gut.

- Volume in bladder is regulated by secreting gas into bladder when it swims deeper and removing gas when it swims up.
  - Physostomous-type fish can gulp air and burp air to regulate volume.
  - Physoclistic-type fish regulate volume by secreting gas from the blood.
- **Gas gland** present in both types
  - Anterior ventral floor of bladder.
- **Rete mirabile** ("wonderful net") is a counter-current system that moves gas from blood to bladder.
- Physoclistic-type fish get rid of gas in bladder through a valve, the ovale.



- Sharks, rays, chimaeras do not have swim bladders
  - They use the liver to regulate bouyancy.
  - High oil content (shark-liver oil), makes liver lighter than water (especially seawater).
  - A 460 kg, 4-m long tiger shark weighs about 3.5 kg in the sea.
  - Bottom-dwelling cartilaginous fish have relatively smaller livers and oil vacuoles, and are negatively bouyant.

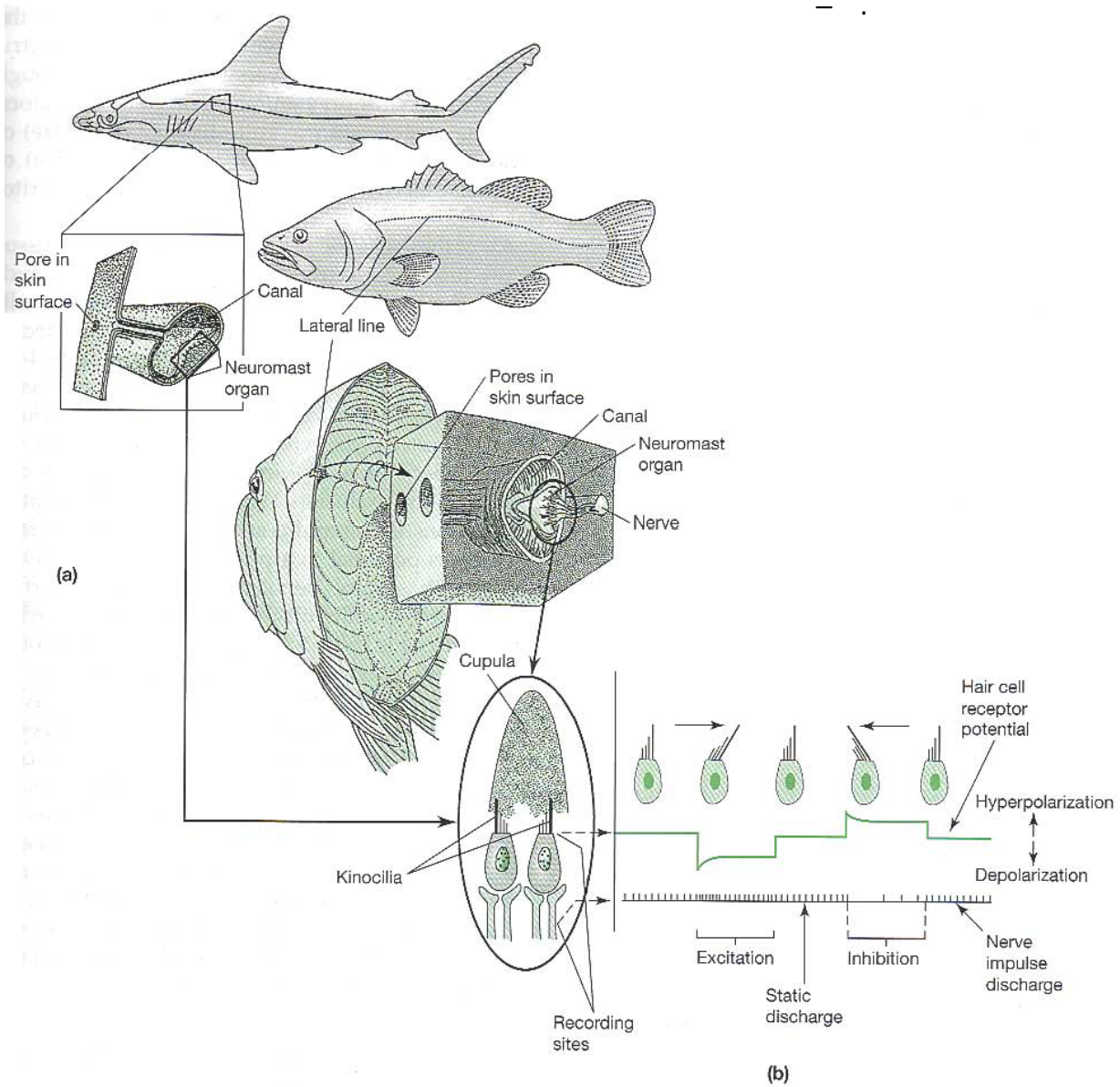
Lateral line system

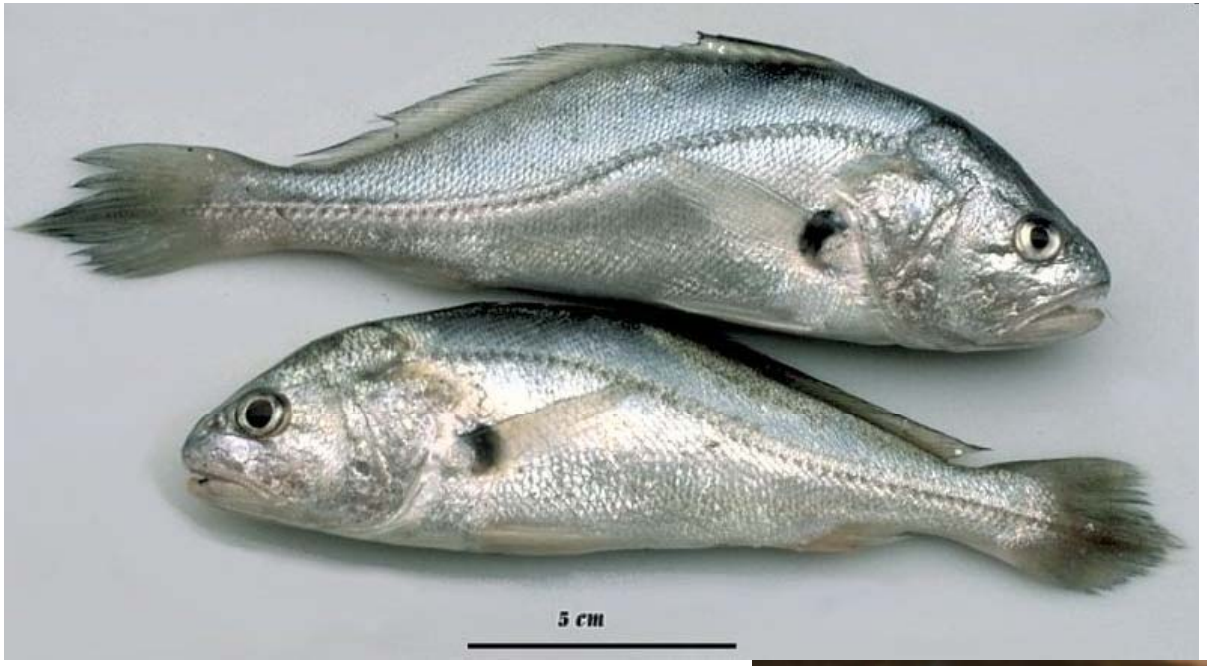
Know how it works;

Know who has it.

- System of integrated mechanical receptors that are sensitive to changes in water pressure.
- Clusters of hair cells form **neuromast** organs, arranged in canals along body and around head.
- Aquatic vertebrates
  - Tadpoles
  - Aquatic frogs and salamanders
  - Fish
  - Not in marine mammals or marine reptiles

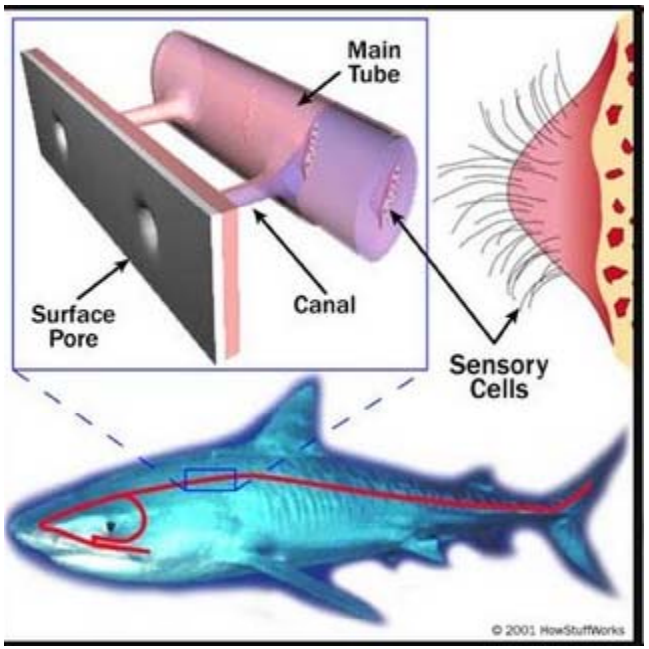
- Hair cells
  - Neuromast organs
    - Series of canals




5 cm

How lateral line works

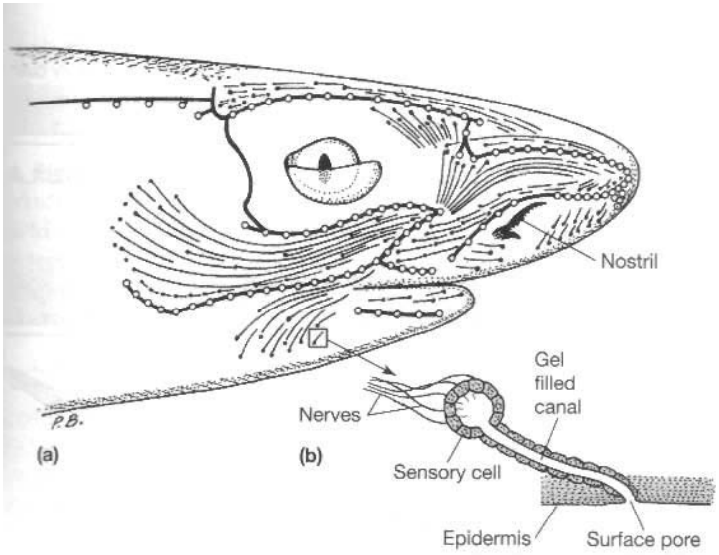
- **Kinocilia** of the hair cells are asymmetrically arranged in cluster of **microvilli**.
- **Hair cells are arranged in pairs**, with kinocilia on opposite sides of adjacent cells.
- This arrangement allows **directional signals**. One nerve transmits from kinocilia oriented one direction, the other nerve transmits from kinocilia oriented the opposite direction.
- The **gelatinous cupula** encases these cells and water pressure on it makes the kinocilia bend.
- Thus, each pair of hair cells works to signal the way the cupula is deformed by water pressure.
- Super-sensitive: Fish and aquatic frogs find insects on water surface by detecting the waves they make.



www.marinebiodiversity.ca/shark/english/ampul.htm

Electroreception

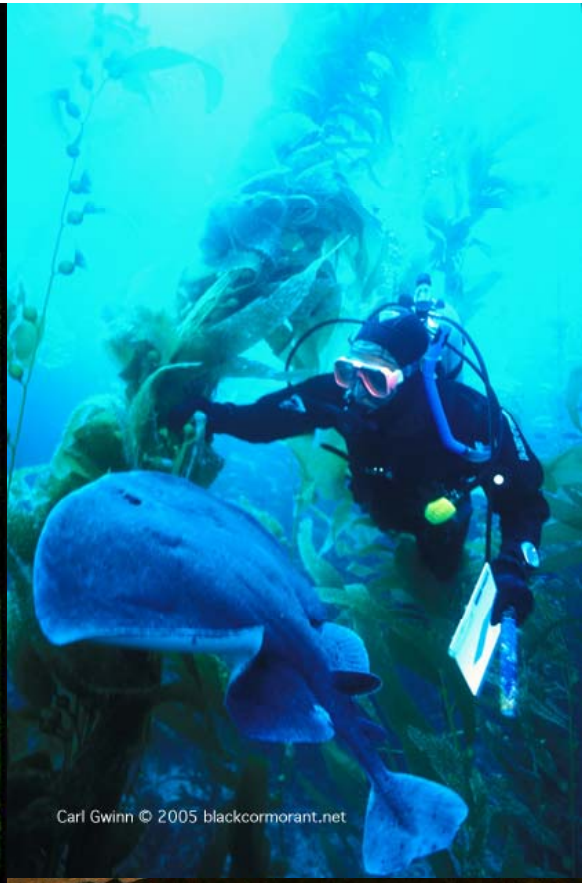
- **Ampullae of Lorenzini**
- Allow detection of electric fields, which are changes in electric potential in space.
  - Present on heads of sharks and rays, some rays have them on fins.
  - The canal runs along under the skin, and is filled with conductive gel; the canal itself is nonconductive.
  - Sensory cell detects difference in electric potential along the canal.
  - These were derived from lateral line cells.
  - They detect 0.01 volt differences
  - Provide a “picture” of electric field surrounding an animal and help sharks detect their prey.
  - This is how sharks find prey hidden under sand because live organisms have electric fields due to muscle contractions, etc.

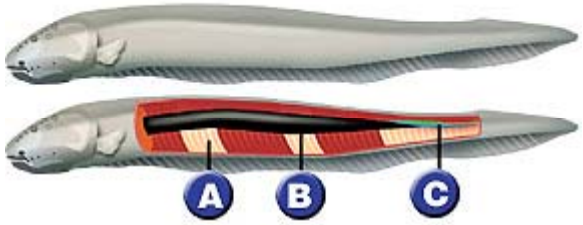


Porbeagle shark

Electric discharge

- Electric eel of South America
- Torpedo ray of Mediterranean
- Electric catfish from Nile River



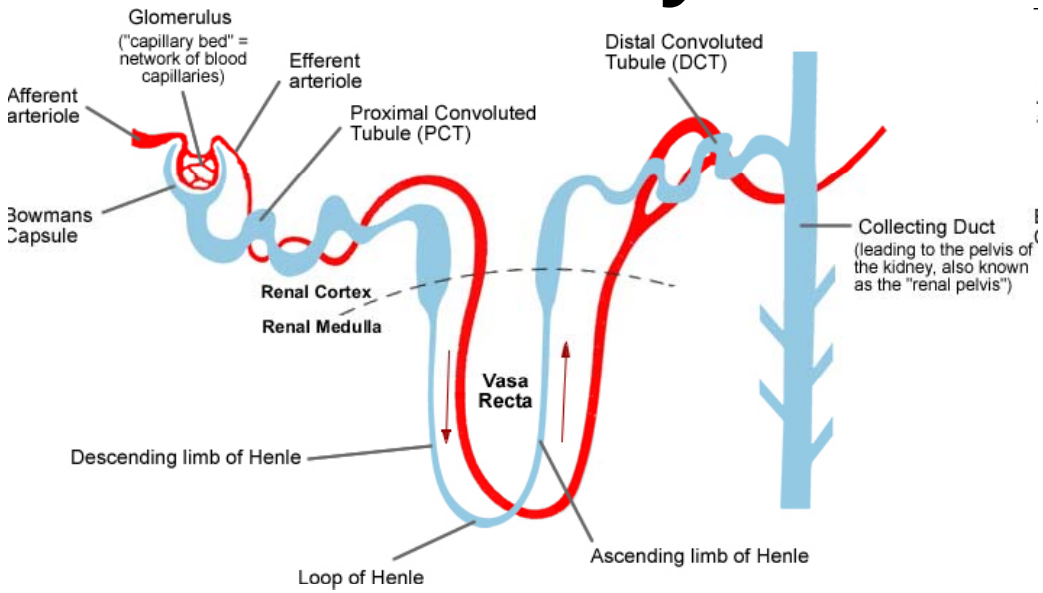


- Electric signals for courtship and territoriality
  - Gymnotidae: weakly electric knife fish (Neotropical)
  - Elephant fish: Mormyridae (African)

Transmembrane potentials in series can create electric potentials of 600 V in electric eel.

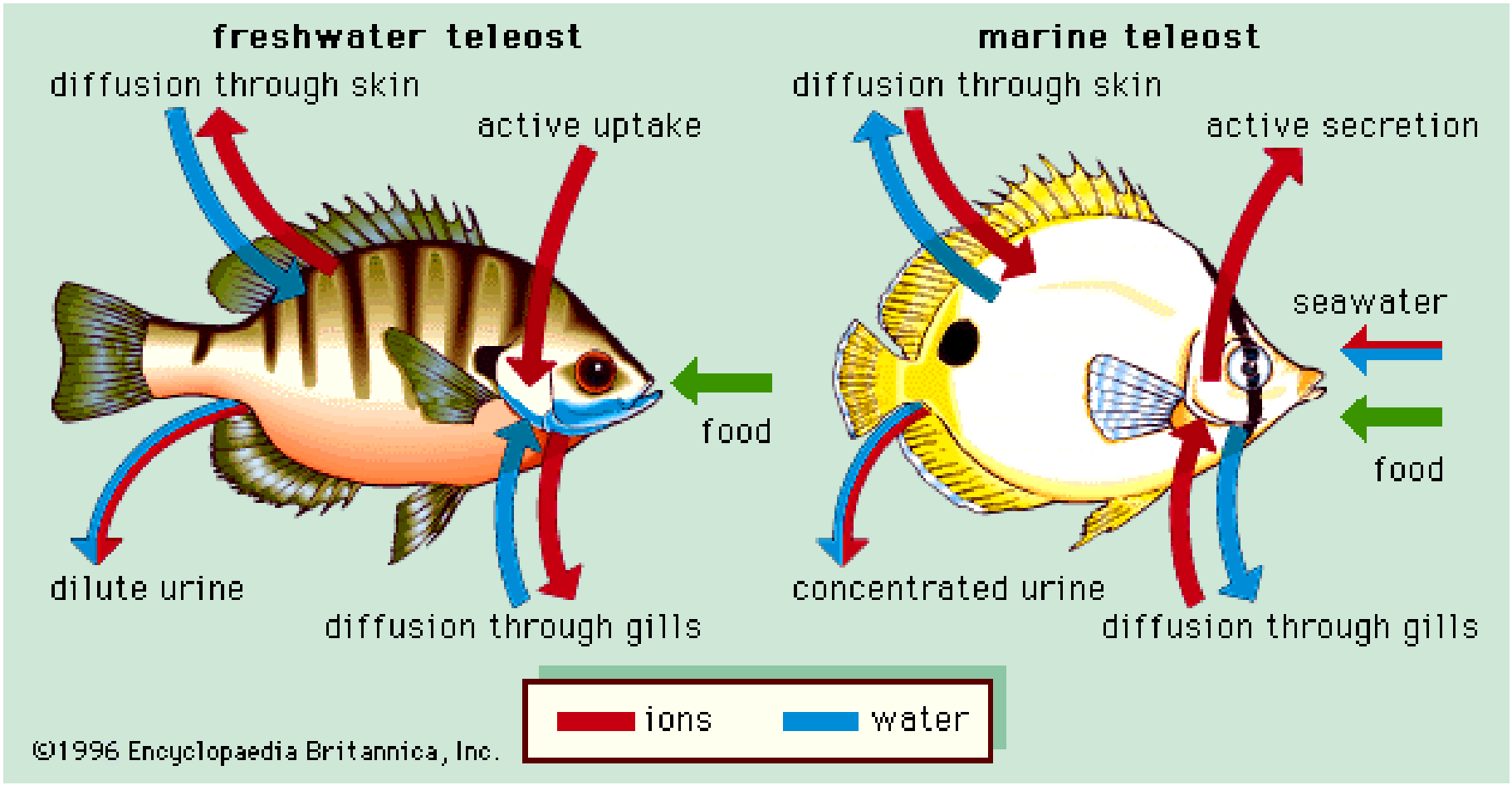
- Modified muscle tissues, called electrolytes, are specialized for creating ion current flow.
- At rest, both sides are -84 mV
- When cell is stimulated, sodium ions flow across membrane making +67mV potential on one side, -84 on other side = 151mV potential across the cell.
- The cells are stacked like batteries in a flashlight. In Electric eel, 10,000 layers can generate a charge of 600 volts.

The vertebrate kidney



- Kidney eliminates ammonia, which is toxic.
- Review of kidneys:
  - Millions of **nephrons** produce urine;
  - Removes water, salts, metabolites, substances from blood;
  - Blood goes through **glomerlus**, a shared, derived feature of vertebrates.
  - Blood pressure forces fluid into the nephron to make ultrafiltrate, which is blood without blood cells;
  - Ultrafiltrate is processed to return glucose, amino acids, water to cirulatory system;
  - The fluid remaining is urine.

- Osmosis: water flows from more dilute into more concentrated solution. Seawater concentration is ~1000 millimoles/kg.
- Marine invertebrates and **hagfishes** have fluid concentration equal to seawater; they are **isosmolal to seawater**.
- Marine teleosts and lampreys are 300-350 mmoles/kg, so water flows out of their blood to the sea.
  - **They are hyposmolal**
- Cartilaginous fish and coelacanth retain urea in tissues, raising osmolality of their blood to a bit higher than seawater. Thus, water flows from sea into their bodies.
  - **They are hyperosmolal**



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- In seawater the challenge to a vertebrate is water going out and salt going in.
- In freshwater the challenge to a vertebrate is water coming in and salts going out.
- GILLS: most of the water-salt exchange takes place through gills, not surprising because they are so permeable.
- Freshwater teleosts
  - do not drink, because they are battling too much water coming in.
  - And they urinate constantly to get rid of water and have large well developed glomeruli in the kidneys.
  - have chloride cells in the gills which take up ions from the water with active transport against the osmotic gradient.
- Amphibians are similar to freshwater fish situation.
  - Amphibian don’t drink and their skin takes up ions.

- Marine Vertebrates: Teleosts and other fishes
  - Kidney glomeruli are small because they do not make much urine, and the urine is very concentrated;
  - Marine teleosts
    - Constantly drinking seawater;
    - Sodium and chlorine are absorbed in gut, and water flows by osmosis into blood;
    - Many species drink >25% of their mass in seawater every day and absorb 80% of the water.
    - To compensate for the salt load, chloride cells in gills pump chloride ions outward with active transport against the concentration gradient.
- Hagfishes
  - Few problems because they are ososmolal.
- Cartilaginous fishes
  - Retain urea in tissue and are slightly hyperosmolal to seawater;
  - Gain water by diffusion across gills and do not drink;
  - Large glomeruli eliminate waste from blood, but gills are impermeable to urea and it is reabsorbed in kidneys.
  - Do NOT have chloride cells to get rid of excess salt
  - DO have rectal gland that secretes fluid isosmolal to seawater, but with higher concentrations of sodium and chloride than seawater.
  - Freshwater sharks and rays have low levels of urea in tissues.