

The  
Sextant



Welcome to The Sextant  
Your Guide to Aquatic Biology  
Biology 450/494  
at Marietta College

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# Aquatic Biology Syllabus

Goals: To learn the unique opportunities for life posed by the aquatic environment and explore the myriad means of exploiting those opportunities utilized by aquatic organisms. To survey the major groups of aquatic organisms and examine their roles in aquatic communities. To be able to recognize on sight important aquatic organisms. To explore some of the unique environmental problems dealing with aquatic environments. To develop *employable skills* in freshwater biological water quality analysis.

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Instructor: Dr. Dave McShaffrey Office: Bartlett 306 Phone: 376-4743

Textbook: [Sextant](#) - McShaffrey (Hypertext - Located on Bartlett Server)

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Lab: Two Optional Texts (choose one of the two, details in class):

An introduction to the aquatic insects of North America. 1996. Edited by Richard W. Merritt and Kenneth W. Cummins. Dubuque, Iowa. Kendall/Hunt Pub. Co.

McCafferty, WP. 1981. Aquatic entomology : the fisherman's and ecologists' illustrated guide to insects and their relatives; with illustrations by Arwin V. Provonsha. Boston, Mass. : Science Books International.

Please wait until instructions are given in class before purchasing either of these books.

You must also obtain a State of Ohio Fishing License.

Attendance: You are expected to attend all class and lab meetings. Absences will likely affect your grade, either directly or indirectly.

Quizzes: Occasional; will cover all previous material and assigned reading for that date. Some quizzes may be take home (i.e. homework). Some quizzes will be on identification of insects and other benthic macroinvertebrates. No make-up on quizzes!

Exams: Two tests and a comprehensive final, make-up by **prior** arrangement or legitimate excuse such as your own death or illness.

Missed Labs: Field trips cannot be made-up. Laboratory work may be made up if specimens are still available and I feel like it. One field trip will take at least 1/2 day; this trip will be either on a weekend or a Wednesday afternoon and will be scheduled in consultation with the class.

Projects (papers): You will write a short (10+ page) paper on an applied aspect of aquatic biology.

Quizzes	10%*
1st. test	20%*
2nd. test	20%
Final	25%
Collection	10% (100 species collected and identified by teams)
<u>Paper</u>	15%
	100% * Component of mid-term grade.

Your final grade will be determined as follows:

A+	97%	A	93%	A-	90%
B+	87%	B	83%	B-	80%
C+	77%	C	73%	C-	70%
D+	67%	D	63%	D-	60%
		F	< 60%		

### Aquatic Biology Schedule

Date	Lecture Topic	Reading	Notes
1/15	Introduction	<a href="#">Physical Properties of Water</a>	
1/15	Physical Properties of Water	McShaffrey, D. and W.P. McCafferty. 1987. <i>The behavior and form of Psephenus herricki</i> (DeKay) (Coleoptera: Psephenidae) in relation to water flow. <i>Freshwater Biology</i> . 18:319-324.	
		<a href="#">Chemical Properties of Water</a>	
1/22	Water Chemistry	<a href="#">Which policies can stop large scale eutrophication?</a> Water Science and Technology Volume: 37, Issue: 3, 1998, pp. 193-200	

[Aquatic Habitats](#)

1/29 Aquatic Habitats [Kemp, JL, DM Harper, GA Crosa. 1999. Use of 'functional habitats' to link ecology with morphology and hydrology in river rehabilitation. Aquatic Conservation: Marine and Freshwater Ecosystems 9:159-178](#)

2/5 Respiration [Respiration in Aquatic Organisms](#)

2/12 Osmotic Regulation [Osmotic Regulation & Nitrogen Excretion](#)  
**Test 1**

[Locomotion in Water](#)

2/19 Locomotion [RIBERA, I, GN FOSTER. 1997. Functional types of diving beetle \(Coleoptera:Hygrobiidae and Dytiscidae\), as identified by comparative swimming behaviour. Biological Journal of the Linnean Society. 61: 537-558. With 4 figures](#)

[The Sensory World of Aquatic Organisms](#)

2/26 Sensory Structures [GAINO, E, M REBORA. 1999. Larval Antennal Sensilla in Water-Living Insects. MICROSCOPY RESEARCH AND TECHNIQUE 47:440-457.](#)

[Feeding in Aquatic Organisms](#)

3/5 Feeding methods used in water [McShaffrey, D. 1992. Comparative functional morphology of larval \*Stenacron interpunctatum\* and \*Rhithrogena pellucida\* \(Ephemeroptera: Heptageniidae\) and \*Ephemerella needhami\* \(Ephemeroptera: Ephemerellidae\) with applications in mayfly taxonomy and ecology. Proceedings of the VII International Conference on Ephemeroptera.](#)

3/9--3/17- SPRING BREAK

Handouts

3/19 Biological Water Quality Monitoring [Water Quality Survey](#)

3/26 Benthic Macroinvertebrates [Role of Biological Criteria](#)  
**Test 2**

3/27 Field - Sampling

4/3 Lab - Sorting/Identification [Local Watershed Action](#)

4/10 Field - Sampling Papers Due

4/17 Field - Sampling

Lab - Sorting/Identification

4/24

Evaluation/Review

Note on late assignments: Assignments are normally due at the beginning of class on the date indicated. As a courtesy, I will extend the deadline to 5:00 p.m. of the same day if and only if you attend ***all*** of your classes that day. I will not tolerate skipping class to finish an assignment. A late penalty will be assessed to all late papers; such penalty will range from 5 to 100% of the grade, at my discretion. If unforeseen circumstances (death in the family, illness, etc.) will cause you to miss a deadline, you must inform me *in advance*, and provide me at that time with paper or electronic copies of the work done to date. The electronic age has provided new and creative excuses for not finishing assignments; I note that these gremlins strike only on the night before an assignment is due, and they are ***not*** justification for failure to complete an assignment which should have been essentially completed at least 2 weeks earlier. If such gremlins do strike, I will allow a 24 hour period to correct them without penalty, if and only if you submit, on time, a recent copy of the essentially completed work. It is your responsibility to maintain multiple backups of all critical work.

As a further inducement to keep things on track, I reserve the right to request, on 24 hours notice, copies of any assignments in progress at any point during the semester. Failure to submit evidence of reasonable progress may result in a late penalty being assessed.

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# The Physical Properties of Water

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Water is an almost magical chemical. Its properties never cease to amaze - imagine a chemical that gets more dense as it cools - until it reaches a point where it rapidly becomes *less* dense! It dissolves many inorganic materials as well as organic ones. Organisms can build macromolecules to attract or repel water as needed simply by varying the charge on side chains. Water exists primarily as a liquid at normal temperatures, yet a significant amount can often be found in the atmosphere. Its density is great enough to support the bodies of many types of creatures, often eliminating or reducing the need for elaborate skeletons. The surface tension of water helps it climb trees and support small organisms. It limits the amount of that notorious toxin oxygen that can reach an organism, yet usually carries just enough O<sub>2</sub> to support cellular respiration. Large bodies of water heat and cool so slowly that they effectively insulate the organisms within them from daily (and sometimes seasonal) temperature changes. And, of course, water and its ability to store and move heat controls weather on our planet.

Often, in our considerations of biological systems, we, being terrestrial organisms, speak of the "problems" associated with living in water. We talk about "adaptations" to aquatic life, about the "pressures" (both real and figurative) of living in aquatic habitats. We use terms like "the cruel sea" or "the cold ocean". We are probably wrong. Life evolved in the oceans and is most at home there. Truth be known, terrestrial habitats are the most difficult and require the most "adaptations", at least in the sense that an adaptation is a modification of some original form. Still, the aquatic world is alien to us, and we will no doubt carry our prejudices and biases with us throughout this course.

## The Water Molecule

Most of the physical properties of water that are of interest to biologists are the result of its unique molecular configuration. H<sub>2</sub>O is, of course, comprised of two hydrogen atoms bonded to a single oxygen atom. Water forms in an exothermic reaction whenever hydrogen and oxygen are mixed and exposed to enough energy to activate the reaction. This reaction has been known since the discovery of the two atoms, but was demonstrated most spectacularly in an experiment carried out by the German government. In 1933, the Germans filled a large envelope with hydrogen, sent it across the Atlantic Ocean to build up a large static electrical charge, and allowed the charge to equalize with a metallic structure at Lakehurst, New Jersey. The static discharge ignited the hydrogen in the envelope with atmospheric oxygen to form water. The main problem with this experiment was that it took place too close to the ground for a really large crowd to see, and, since this was before television, we had only radio reporters to relay the observations to scientists around the world. However, since there was a loss of life in the incident, some reconstructionists propose that this elegant experiment was in fact nothing more than a terrible tragedy. Since the German records were lost in the war, we may never know the truth.

Once combined, the water molecule is a strange beast. The oxygen "side" of the molecule has a slight negative charge, while the hydrogen "sides" are slightly positive (Fig. 1). This forms a *bipolar molecule* that can bind the oxygen side loosely to a positively charged ion or molecule, and the hydrogen side to a negatively charged ion or molecule, thus obeying Abdul's Law that opposites attract (Abdul, P. 1990, Chrysalis). This explains many of the unique properties of water. It dissolves so many different things because it can dissolve anything with an ionic charge - positive or negative. It is so dense because under normal circumstances the adjacent molecules are also water molecules and the oxygen on one water molecule binds loosely to the hydrogen on the next, and the binding pulls all the molecules together, packing them in. Surface tension is high because of the attraction of the molecules.

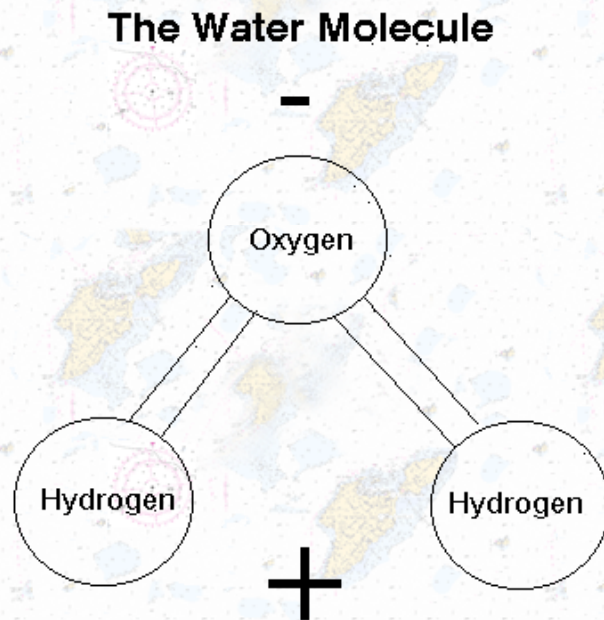


Figure 1. The water molecule, showing positive and negative polarity

## Surface Tension, Hydrophilic and Hydrophobic Interactions

Water binds to *hydrophilic* (water-loving) surfaces because such surfaces have slight electrical charges; it beads up on *hydrophobic* (water-hating) surfaces because they have no charges and the water would rather mingle with itself than mess around with something that has no charge. Oil, for instance, is beautifully balanced ionically, and, you know, oil and water just don't mix. Exxon demonstrated this eloquently in 1989 with a large-scale experiment in Alaska. When some objected that sure, it works in Alaska because it's so damn cold up there, Exxon promptly repeated the experiment (though on a smaller scale) at sites all over the United States. Ironically, although oil and water don't mix, crude oil does mix with the skin oils painstakingly groomed into the fur of sea mammals and the feathers of sea birds, where the natural skin oil waterproofs the keratinaceous outgrowths and allows them to trap air, which acts as an insulator. Crude oil, however, mixes with the skin oils and mats the hair (feathers) down flat, eliminating the air space and the insulation. And, of course, the oil just tastes yummy when it sits in the belly of some poor critter that tries to lick it off so it doesn't freeze to death. Again, Exxon is currently conducting research into these effects.

Detergents destroy surface tension by insinuating their ions among the water molecules and binding them together more loosely than they would normally bind. In your washer this is good, because the detergents allow the water to get in and lift out the soils. In a stream, this is bad, because all the water striders suddenly sink.

Other organisms use "detergents" in creative ways. For instance, the whirligig beetles (Gyrinidae) secrete a *surfactant* - a chemical that reduces surface tension - behind them. They are then "drawn" forward by the surface tension. Whirligig beetles are unusual in several instances. They have 2 *pairs* of compound eyes, one pair above and one pair below the water. They also use chemicals other than surfactants. They have an aggregation pheromone that supposedly smells like *Juicy Fruit*<sup>™</sup> gum (the gum can be used to attract the beetles), and they smell like ripe apples (a defensive secretion). They use echolocation to find each other, avoid obstacles, and find food.

Organisms that exploit the surface tension of water are numerous. Some use the surface tension as a platform to support their weight above the water; others suspend themselves from the surface of the water. For small organisms, the surface tension of water creates a significant barrier to their movement in or out of the water. The trick in dealing with surface tension is to fashion biomolecules to interact with the water in an appropriate way. Add positive and negative ions to your molecule in the right places and you create a *polar molecule* which will be hydrophilic (the water would rather bind to it than to other water molecules); eliminate all ionic imbalances and you create a hydrophobic molecule which will not interact with water. Vaseline and waxes are examples of hydrophobic molecules; organisms often use waxes to make a surface hydrophobic.

The interplay of hydrophobic and hydrophilic surfaces with water can perhaps best be seen by examining mayflies. These organisms have aquatic larvae with hydrophilic surfaces. These surfaces allow the larva to exchange gasses (O<sub>2</sub>, CO<sub>2</sub>) with the surrounding water, which can come very close to the hydrophilic skin. At maturity, the larval mayfly molts to the winged *subimago*, the stage that must break through the water's surface. The subimago is covered with small waxy hairs and beads that are hydrophobic. The subimago floats to the surface and is literally pushed out of the water as the polar water molecules attempt to reform behind the subimago. The subimago can float comfortably on the surface of the water for several seconds - long enough to provide a target for trout, and the basis for fly-fishing - before taking off. It will fly to streamside vegetation and molt *again*; it is the only

insect to molt once it has reached the winged stage. This second molt gets rid of the awkward, heavy, waxy coat of the subimago. The adult mayfly is quicker, but must avoid getting too close to the water. Some mayflies that do come close to the water during their later mating flights may retain some parts of the body (particularly the underside) in a hydrofuge (hydrophobic) state. See the paper by Edmunds and McCafferty (1988) for more details on this interesting transition.

On the surface, water striders (Fig. 2), Collembola, and a host of other small animals try to *avoid* making a transition - that is, sinking. They all have hydrophobic bodies with one exception - the claws. The claws are hydrophilic and penetrate the water surface, allowing the animal to "get a grip" on the water surface. Vogel (1988) has constructed the "Jesus Number" - an index of the practicality of an organism walking on water:

$$J_e = \frac{T}{\rho l^2 g}$$

T = surface tension

(0.073 Newtons/meter in freshwater,

0.078 N/m in saltwater)

p = density of organism

(kg m<sup>-3</sup>)

l = length (perimeter) of organism in contact with water

(m)

If  $J_e$  is greater than 1, it is possible for the organism to walk on water. We won't do anything much with this equation; other than to note that the limits on an organism are primarily a function of its size, since surface tension, gravity and density are all pretty much fixed.

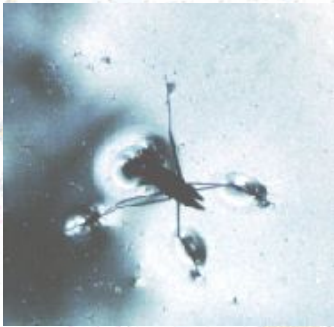


Figure 2. A water strider on the surface. The water displaced in the "dimples" on the surface of the water weighs the same as the insect. Hydrophobic hairs on the legs do not penetrate the water surface; the surface tension holds the water together and the water surface bends rather than breaks. An illustration of the "Jesus number"!

Other organisms suspend themselves from the surface. Mosquito larvae, for instance, have hydrophilic bodies with a fringe of hydrophobic hairs near the breathing tubes at the posterior end of the body. The hairs can be bunched into a small tube and "punched" through the surface (or withdrawn). On the surface, they spread out and anchor the organism to the surface, and the larva is then able to breathe air from the atmosphere. One method for dealing with such larvae is to cover the surface with oil or detergents. The oil will smother the larvae since they cannot anchor in the oil layer, which is also hydrophobic. The detergent, of course, will lower the surface tension (the numerator in the number  $J_e$ , above).

## Density and Buoyancy

Density changes in water as it warms or cools have profound impacts on aquatic organisms. Density is also a major component of two other important parameters - *dynamic and kinematic viscosity*. All three of these parameters decrease (usually) with *increasing* water temperature. Dynamic viscosity represents the "stickiness" of water - how easily it flows (molasses has high dynamic viscosity). Kinematic viscosity is dynamic viscosity divided by density, a useful parameter in some calculations because it eliminates the effects of mass. It is easier to swim (or move blood) in warm water, but it's harder to float.

Floating in H<sub>2</sub>O is made somewhat easier due to the density of water. Most organisms have bodies that are at least 90% water, which means that at least 90% of their body weight will be offset by the weight of the water around them. It's that last 10% that is critical. Organisms that live on the bottom of a body of water are called *benthic* organisms. Efficient locomotion for them often entails walking or crawling on the substrate. Just as on land, in order to walk on the bottom, they need traction, and traction is largely determined by weight - or, more accurately, the downward pull on the body caused by gravity, which, as we have just seen, is largely offset by water for aquatic organisms. For instance, try walking in a pool. The shallower the water, the easier it is to walk. As depth increases, so does the effort you must put into walking. This is partly due to the increased effort it takes to move the water out of your path, but you'll also notice that in deep water, over chest height, you have a little more "bounce" in your step, and it gets hard to walk. Benthic organisms usually deal with such problems by making that last 10% of the body as dense as possible; they may have heavy shells, massive bones, or even construct cases out of rocks to carry around.

Swimming organisms (*nekton*), or floating organisms (*plankton*), have the opposite problem, and their solution is similar. They make the remaining 10% of their bodies as light as possible. Fats and oils are two biological molecules that are less dense than water and allow some organisms to float. Fats and oils are also a storage medium for energy and can be used for insulation in warm-blooded animals. Sharks have large, oil-filled livers which help them float; Flipper and other porpoises kill sharks by striking them in the liver with their snout, rupturing the liver. Trapped air is also effective as a float, of course. The Portuguese man-of-war has a gas float; waterfowl float high in the water due to air trapped in their feathers and the hollow bones in their skeletons. Fish have air-filled swim bladders (some completely isolated from the outside atmosphere and regulated through gas exchange with the blood); bladderworts (a floating plant) have air filled cavities (bladders).

Very small organisms also try to manipulate their density, but their efforts are often more difficult to explain. Diatoms, for instance, must stay near the surface to obtain enough light for photosynthesis, yet they have a heavy shell of silica. They offset the shell to some extent by a store of oil, but they still "worry" about sinking. Fortunately, the world of very small organisms is governed by different rules than the world we live in. To them, water is more like molasses and sinking rates are very small, often small enough to be offset by local currents caused by the water heating and cooling. The heating and cooling of the water also changes its density, and, for small organisms in particular, this is not a trivial matter. The change in density of water from 4° C to 25° C is large enough to mean the difference between floating and sinking in many organisms with densities near that of water. It is easier to float in denser water, and fresh water is most dense at 4° C (Fig. 3). Salt increases density of water (Fig. 4); it is easier to float in salt water as opposed to fresh water, and easier still in hypersaline environments such as the Great Salt Lake in Utah. It is not unusual for populations of small organisms to undergo seasonal morphological changes at least partially in response to temperature induced water density changes; one of the best examples is *Daphnia* (see

## Density of Freshwater

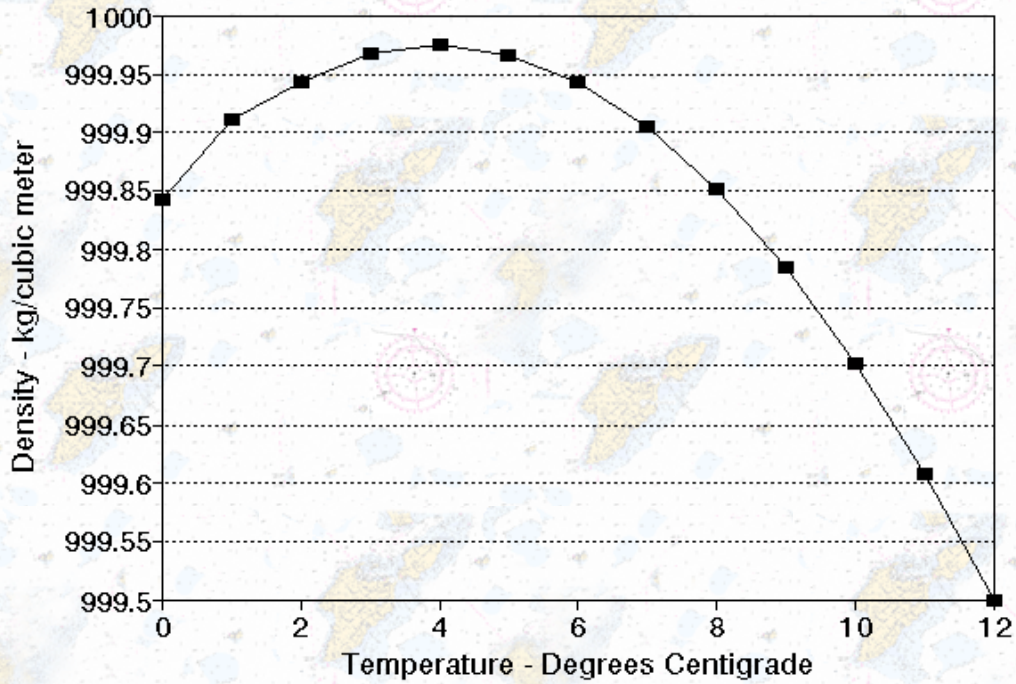


Figure 3. Relationship of water temperature to density for distilled water.

## Effect of Salinity on Density

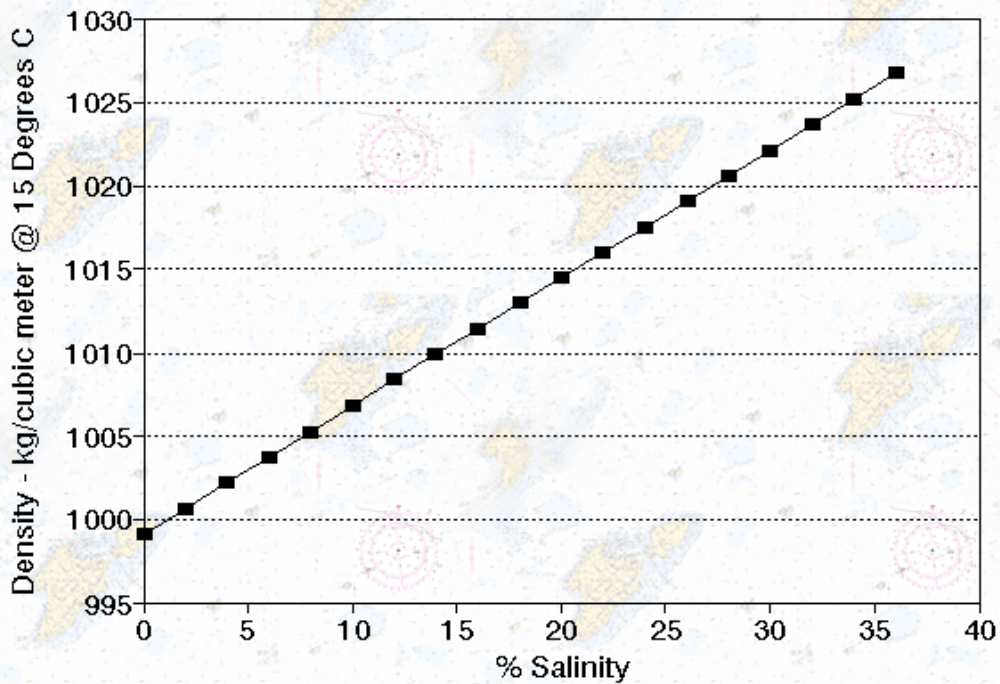


Figure 4. Relationship between percent salinity and density of water at 15° C.

The general equation governing sinking rates in water for small spherical organisms is given below:

$$U = \frac{2a^2g(p - p_0)}{9\mu}$$

Where  $U$  is equal to the sinking rate,  $a$  = the radius of the sphere,  $g$  is the gravitational constant ( $9.8 \text{ m s}^{-2}$ ),  $p$  is the density of the organism,  $p_0$  is the density of the medium, and  $\mu$  is the dynamic viscosity ( $\text{kg m}^{-1} \text{ s}^{-1}$ ). Note that if the density of the medium is greater than that of the organism,  $U$  will be negative - a "floating" rate.

## Boiling and Freezing - Temperature and Heat

The fact that ice floats is due to the sudden reversal at  $4^\circ \text{C}$  of the general trend of decreasing temperature = increasing density. This is due to the ice crystals forming; the average distance between the water molecules in ice is greater than it is between water molecules at  $4^\circ \text{C}$ . The farther the molecules are apart, the fewer will fit in any given volume - that means less density (are you starting to appreciate density yet?). Ice formation is discouraged by molecules that get in the way of the water molecules - salt ( $\text{Na}^+$ ,  $\text{Cl}^-$ ), ethylene glycol, etc. These molecules lower the freezing temperatures of water, and allow some organisms to exist below the "freezing point" (of pure water). Furthermore, the freezing of water releases large amounts of heat. This means that water is very temperature stable at the freezing point. Winter weather is moderated to a great extent by this factor. Winter temperatures will stay near  $0^\circ \text{C}$  until all the local water is frozen. By the same token, it takes a lot of energy to melt ice, and local temperatures will not warm up until the ice is melted. You are probably more aware of the other end of the spectrum - when water boils. As you well know, the temperature of a pan in which water is boiling will not exceed  $100^\circ \text{C}$  until all the water has boiled out. This means that you can boil water in a paper cup - but watch out when the water is gone!

Boiling is the rapid evaporation of water. Unlike freezing, which does not occur until all the water is at  $0^\circ \text{C}$ ; evaporation can occur at any temperature as long as the atmosphere is not already saturated with water. The ability of air to hold gaseous water is also correlated to temperature; the warmer the air, the more water it can hold. In the winter, a house takes outside air, which is cold, and warms it. This warmer air can hold more water, and since it is "short" of water, water will evaporate from moist areas in the house (plants, people, etc.) more quickly. Therefore, you have to water plants more often, and you are more likely to catch cold, since your respiratory linings can dry out and be unprotected from viruses. When warm air is cooled, it can no longer hold water and water comes out of the air. If the ground cools off, it will pick up  $\text{H}_2\text{O}$  from the adjacent air (dew); as water vapor rises through the atmosphere it cools and the water condenses and falls to the ground (fog, clouds, rain). Moist air also holds more heat and "feels" warmer to us (although moist air and dry air at the same temperature are *at* the same temperature we perceive the moist air as "warmer").

The large number of molecules per unit of volume (density) of water means that the overall kinetic energy of all those molecules combined (heat) will also be large. In addition to the "extra" heat that must be added or extracted when changing the physical state of water from solid to liquid to gas (or gas to liquid to solid); it takes a lot of energy (heat) to change the overall kinetic energy of the densely packed water molecules. It is important to realize the difference between heat and temperature, temperature is a *quality*, heat is a *quantity*. Temperature measures how fast (how much kinetic energy) a group of molecules is moving; heat measures how many molecules have that energy. Water, being dense, has a lot of molecules, therefore, a lot of heat, at least compared to air. The specific formula for heat is:

$$H = m \times t \times sh$$

Where  $H$  = heat,  $m$  = mass (grams),  $t$  = temperature (degrees C), and  $sh$  = specific heat, a constant that varies from material to material (and also varies with temperature).

We measure heat in *calories*, with a calorie being defined as the heat needed to raise one gram (one ml) of  $\text{H}_2\text{O}$  at  $15^\circ \text{C}$  one degree C. Thus, substituting 1 for  $H$ ,  $m$ , and  $t$  in the equation above, we can see that the  $sh$  for water at  $15^\circ \text{C}$  is also equal to 1. The same amount of heat will have a different effect on other materials, or on water at different temperatures. The calorie mentioned above is different from the caloric values assigned to food; these are roughly 1,000 calories and are thus known as *kilocalories* or *Calories*. You should also be aware that the calorie does not exist in the SI; it is replaced by  $\text{J kg}^{-1} \text{K}^{-1}$ , or the number of joules it takes to raise 1 kilogram one degree Kelvin (the SI system is the official system of science and is not the same as the metric system, although it is closer to the metric system than the English system is). Water has more heat than air not only because it is more dense, but also because it has a higher specific heat - that is, if you had a kilogram of air and a kilogram of water, it would still take more heat to warm the water one degree than the air.

The high specific heat of water, coupled with the amount of heat absorbed or released in changing its physical state, combined with the vast quantities of water on the planet, means that water plays a major role in climate and weather. Water is the greatest sink and conveyor of solar energy reaching the earth. For instance, heat carried by the Gulf Stream from the warm tropics keeps England and parts of Europe much warmer than they would otherwise be given their latitude. Organisms living in oceans may only encounter a  $2 - 3^\circ \text{C}$  temperature change over their lifetimes. Organisms living in sizable (pond-size) bodies of water do not experience diurnal temperature changes (except at the surface and edges), and only a  $30^\circ \text{C}$  change seasonally, spread out over a period of weeks. Terrestrial organisms may experience a  $30^\circ \text{C}$  temperature change daily - especially in deserts where there is little water vapor in the air to block heat transfer - more on that later.

## Water and Light

Water interacts with the light that strikes it. These interactions are very complex, and extremely variable, and we will only briefly discuss them here. Pure water tends to absorb long wavelength light (reds, infrared) strongly, and allows short wavelength light to pass (blues, ultraviolet). Any suspended or dissolved particles in the water increase absorption, particularly of UV (ultraviolet) light. Since the concentration of such suspended or dissolved materials varies greatly, few general principles exist. However, it is generally accepted that at depth, particularly in the ocean, the light has a bluish cast and underwater photography relies heavily on flash or artificial light to image the reds and oranges that otherwise appear black at depth due to the lack of those colors in the ambient light. Fish and other organisms that appear brightly colored to us when brought to the surface may actually be quite drab in their native habitat. This factor cannot be overemphasized when exploring the biological significance of color in aquatic organisms - they must not be judged in terms of their surface coloration (also, unless you know something about the color perception of the organisms in question, coloration is meaningless).

Water color itself is also a tricky subject. Pure water appears clear. Its surface may take on the appearance of the sky through reflection, or of the substrate underneath due to refraction, and the two - reflection and refraction - interact as the viewer changes angles relative to the water surface. Water may also take on the color of materials suspended in it, including algae and sediment. The lovely color of the Ohio River is not a reflection of the sky (that would make it gray), or even a refraction of the bottom (which you can't see even in water centimeters deep).

It should come as no surprise that water transmits the same colors - blues - as are vitally critical in photosynthesis; after all, photosynthesis evolved in water. Our traditional view of the two-peaked photosynthetic absorption curve, with peaks in the red and blue, is somewhat distorted by the presence of accessory pigments that increase absorption of long-wavelength light. Also, remember that light passing through natural water is also being absorbed by photosynthetic organisms, which means that there is competition for light at greater depths by photosynthetic organisms.

All in all, however, the color of light in water is not as critical to photosynthetic organisms as the intensity of that light. Near the surface there may actually be too much light; at depth there may not be enough. Of crucial interest to us will be the *phytoplankton*, those organisms such as algae that photosynthesize, yet are at the whim of the currents as they lack the ability to swim strongly. The depth at which a photosynthetic organism's rate of photosynthesis balances its rate of respiration is known as the *light compensation point* (LCP); a small organism with little stored energy reserves cannot survive long if it sinks below its LCP. Note that the LCP will vary by species and that dissolved or suspended materials (including other phytoplankton) in the water column will absorb light and raise the LCP for all species - the LCP in the Caribbean is measured in tens of meters; in the Ohio River it is measured in centimeters. The cyanobacterium *Plectonema woolei* in turbid Lake Erie has virtually all the known accessory pigments. Grown under low-light conditions (it can grow in a refrigerator, apparently getting enough light when the door is opened occasionally) it is black in color. Its LCP in Lake Erie is often about 10 m, where visibility to the human eye is measured in cm.

Modification of the LCP of many organisms will, of course, have profound impacts on the ecosystem. One of the more sinister projections of a "nuclear winter" scenario is the decreased light penetration due to smoke and dust in the atmosphere. This would raise the LCP to near (above?) the surface of the ocean, and such effects would persist for a longer period of time than the small phytoplankters, with their tiny energy reserves, could hold out. They would die, and since they produce a major portion of the O<sub>2</sub> in our atmosphere .....

As light passes through water in the air, similar effects are seen. Water vapor in the air absorbs infrared (IR) strongly, while allowing UV to pass; thus, a cloud blocking the sun causes us to perceive a drop in temperature, and it is possible to get sunburned on a cloudy day. Water vapor also absorbs heat trying to leave the Earth and radiate out into space. One reason that deserts are cold at night is that there is little water vapor to block heat loss at night (the same heat loss occurs during the day, but is offset by incoming solar radiation, *insolation*); for the same reason, it gets cooler on clear nights than on cloudy ones. Water plays still another role in the global heat balance. Light colored objects reflect light (and heat); thus clouds, ice and snow, which are light-colored (have a high *albedo*), reflect heat back into space and tend to cool the planet. If you have a lot of snow, as during an ice age, this effect can feed on itself: the snow reflects the heat, which cools the planet, which allows more snow to form, which further cools the planet, and so on. The reverse takes place if things warm up, an important consideration in our examination of global warming.

## Pressure

We have not mentioned pressure yet, primarily because it is of less concern to aquatic organisms than you might think. Although there are real physical/chemical effects that occur at great pressures, the biggest problems that organisms face is a *difference* in pressure, and most organisms deal with this very effectively. Pressure is caused by the weight of fluids (air, water), above you. At sea level, we measure pressure as one atmosphere (we'll avoid the messy SI units, pascals m<sup>-2</sup>, for now). That is the cumulative pressure of *all* the air. By the time we go only 10 m underwater, the pressure doubles to 2 atmospheres, and it increases by 1 atmosphere every additional 10 meters. While water is (nearly) incompressible, air is not, and air at atmospheric pressure taken underwater soon begins to compress; here is where most pressure-related problems come into play. An organism using air for buoyancy will find that air compressed as it sinks, further decreasing buoyancy and thus increasing the sinking rate, leading to a positive feedback loop. Any organs (lungs) containing air will be crushed as the air inside can no longer support them. Rising through the water column can have the opposite effect: uncontrollable ascent rates and explosion of air containing tissues. Organisms with air-containing organs are well advised to limit their vertical movement in the water column, or to enclose their air in a hard structure, such as the shell of a *Nautilus*. Fish caught in deep-sea trawls often explode as their swim bladders expand when they are forcibly brought to the surface. Whales, such as the sperm whale, and other organisms that routinely dive to great depths and return to the surface to breathe, have other adaptations that prevent damage (such as the lungs being small relative to the overall mass of the whale).

Humans entering water without any special equipment are limited to relatively shallow depth (30 m) for short periods of time (60 s). This was changed by the introduction of compressed air. Compressed air has enough pressure of its own to compensate for the pressure of the water, and allows the lungs to expand normally. As long as the compressed air is the same pressure as that of the surrounding water, and as long as the air can move through all air passages in the body freely (there is no congestion in the sinuses or eustachian tubes), all is well - up to a point. If the diver ascends without breathing normally, the air in the lungs is at a greater pressure than the surrounding water, and the lungs expand to the point that the thin tissues of the alveoli rupture, leading to air in the blood (and blood in the lungs), and probable death by air embolism. This effect is particularly pronounced in shallow waters, where a change in depth of a few feet without normal breathing can cause an embolism, often without accompanying pain, thus making it very dangerous. Most SCUBA (self-contained underwater breathing apparatus) classes simply involve ramming home the simple rule of breathing normally at all times, and allow the diver to become proficient enough that panic is not likely to occur and cause the diver to forget that simple rule.

From a physical standpoint, a human with compressed air could go to the deepest points of the ocean. From a physiological standpoint, however, this is not practical for several reasons. One is that oxygen is toxic, and the critical factor is the partial pressure of  $O_2$ . Without going into details, this means that as depth increases,  $O_2$  becomes more toxic. To avoid this, divers going to depths below 100 m routinely use gases with less than "normal" 21% oxygen. Nitrogen, normally inert in the body, causes neurological effects (Nitrogen narcosis) at depths greater than 100 m, and is often replaced by helium (which carries body heat away so effectively that special provisions must be made to warm the diver - He also causes "Daffy Duck voice"). Helium-oxygen mixtures have been tested to depths of about 600 m. Because of the costs of the specialized equipment and support teams, as well as the problem of decompression (see below), 600 m may be a practical limit for humans in the ocean. Below that depth humans need to be encased in structures (submarines, hard diving suits) that bear the pressure of the water, leaving the human at normal pressure. Recent advances in electronics have also made remotely piloted vehicles (ROV's) practical for work at great depths; witness the recent success of the ROV *Jason* in the discovery of the *Titanic*.

A further complication of diving with compressed gases is that the gasses form tiny bubbles in the blood under great pressure. As the diver ascends, these bubbles come out of solution and grow rapidly, not unlike the way a carbonated beverage bubbles when you remove the top (ever play beer hunter?). Like such beverages, agitation increases bubble formation, and the bubbles are most likely to form at the joints. The bubbles block blood flow and pinch nerves, causing the victim great pain, particularly at the joints. Victims often assume a bent, fetal position, giving rise to the common name for this syndrome - the bends. It often afflicted workers in caissons, pressurized structures built on the bottom of a body of water to facilitate construction work (bridge pylons, tunnels). A celebration of the completion of one such structure (a tunnel under the river in New York) turned out rather flat when the politicians found that the champagne wouldn't fizz under pressure. Fortunately, the local populace was treated to a joyous moment sometime later, when the politicians emerged and their otherwise boring speeches were punctuated by enormous belches fueled by great quantities of now depressurized champagne. Treatment for the bends requires repressurization in a recompression chamber, a fact known to all fans of *Sea Hunt*, *Flipper*, or *Voyage to the Bottom of the Sea*. Avoiding the bends requires carefully planned decompression stops on ascent, allowing the gasses to be vented slowly, a fact also well known to most fans of the above shows. Lesser known is that most sport divers are counseled to avoid decompression by planning no-decompression dives; these carefully limit the times spent at different depths to avoid build-up of  $N_2$  in the blood. A no compression dive might mean being able to stay down 1 hour at 10 meters, but only 15 minutes at 20 meters. Time spent ascending, descending, on the surface, and flying on airplanes must also be considered. The charts formerly used to calculate no-decompression (and decompression) dives are being replaced by microcomputers worn by the diver which sense depth, altitude, and time, and advise the diver accordingly. Lesser known still is that the research on which these charts are based was performed using US Navy divers during and after WWII. These *men* were usually about 2 m tall and had virtually no body fat, consequences of stringent recruiting practices and physical training. Recent research has shown that factors such as sex, size, and body fat can influence onset of the bends. Body fat, in particular, has an aggravating effect on the bends, and the relative safety of sport diving up until this time has been due to the extreme conservatism of the Navy scientists (who also fudged the data so that the dumber of these big guys could still use the tables in an era when an electronic calculator filled a room). The gender bias of the study was understandable given who was developing these tables, and what their motivation was; what is inexcusable was the length of time it took to replicate these studies with women (and people of different sizes and fat contents). Such data is being gathered and incorporated into such tables now.

## Drag

A final physical topic related to water is the cost of moving through it. We have already seen that vertical movement - buoyancy or sinking - is easily accomplished by manipulating density and letting the forces of gravity do the rest. Horizontal movement, or vertical movement against the forces of gravity, is more complex. Two things must happen when an object moves through water. The water in its way must be moved, and the water "sticking" to it must be sloughed off. The first of these is a function of speed, size, and shape of the organism and is called *pressure drag*; the second is a function of speed and the amount of surface area present and is called *friction drag*; together they are called simply *drag*. As speed increases, or as size of the organism increases, friction drag becomes less important than pressure drag. This is due to the fact that friction drag is proportional to the surface area of the organism, while the amount of water that must be moved is more proportional to the volume, and, as size increases, volume increases more than surface area. Friction drag is also more important in air than in water, and at slow speeds in relation to high speeds. The type of drag that predominates can have dramatic consequences for the organism. For instance, we live in a world dominated by pressure drag, and the way to reduce pressure drag (thus increasing efficiency of locomotion) is to *streamline* an object, making it present a small profile to the fluid the object is moving in - a Corvette has less pressure drag than a Mack truck, even if both were the same size. However, streamlining also increases friction drag. In our world of big things and high speeds, friction drag is by far the smaller coefficient of overall drag and can be ignored, but many small organisms live under the reverse conditions and cannot afford to overlook friction drag.

How can we tell which type of drag will be most important to an organism? Fortunately, a simple mathematical relationship exists, the *Reynolds* number (Re):

$$Re = \frac{\rho l U}{\mu}$$

Where  $\rho$  = density of the fluid;  $l$  = characteristic length of the object;  $U$  = the speed (of the object or the fluid or both); and  $\mu$  = the dynamic viscosity. The length is somewhat arbitrary; it is usually the length normal to the flow, i.e. the diameter of a sphere, the diameter of a cylinder normal to the flow, the length of a cylinder parallel to the flow. It is important to set up the equation so that all of the variables are in the same units - that is, you can't have a speed measured in meters per second and a length measured in millimeters. Under these conditions, Re is a dimensionless index (try it, all the dimensions cancel out). If  $Re < 1$ , then friction drag predominates and flow is smooth or *laminar*. Between 1 and 1000, there is a transitional zone, where both factors are important but hard to predict (unfortunately, most organisms spend at least part of their lives in this zone), and flow may become *turbulent* (turbulence is a major factor in pressure drag). Above 1,000, pressure drag predominates, and you would expect to see streamlined structures (which work, in part, by avoiding turbulence which predominates at high Re).

Note the effect of changing any variable. Water is more dense than air, it leads to a bigger Re (the effect of the dynamic viscosity is swamped by the larger values for density); longer organisms will have a larger Re; larger Re's will predominate at higher speeds. Life at low Re is a strange world; recent experiments to simulate low Re conditions for humans used lime Jell-O (high viscosity) and have been perverted into a strange ritual staged as "entertainment" where opponents attempt to find optimum movement strategies for the low Re and best their opponents in physical contests. Apparently,

wearing a minimum of clothing has been found to be adaptive under such conditions, perhaps clothing increases friction.

The Reynolds number has far-reaching effects, and we will discuss many of them this semester. One we have already discussed is sinking rates:

$$U = \frac{2a^2g(p - p_0)}{9\mu}$$

Once the sinking rate is calculated, it is necessary to use the value of U to calculate a Re for the spherical organism. If the  $Re > 1$ , the calculated sinking rate may not be accurate, since the equation for sinking rate assumes the laminar conditions of low Re. If the Re is greater than 1, turbulence may develop, increasing pressure drag and reducing the sinking rate. There are formulas for the sinking rate of larger (or faster sinking) objects, but we won't go into them here.

## Further Reading - Physics

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[Craig, Douglas A.](#) Some of what you should know about water or, K.I.S.S.\* for HYDRODYNAMICS (\*Keeping It Stupidly Simple) Department of Entomology, University of Alberta, Edmonton, CANADA T6G 2E3

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# The Chemical Properties of Water

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In examining the physical properties of water, we have, in a way, begun discussing the chemical properties of water. We have already seen that  $H_2O$  is a polar molecule (Fig. 1), with a slight positive charge near the hydrogen and a slight negative charge near the oxygen. These subtle charges are the key to understanding most of water's chemistry. We have seen that polar and ionic molecules can dissolve in water, while ionically balanced compounds, including many hydrocarbons, are insoluble in water. If these chemicals are on the surface of a solid, they will determine whether that solid is hydrophobic or hydrophilic. Overall, however, the chemistry of water is largely a study of what is dissolved in it, and we will turn to those matters now.

**The Water Molecule**

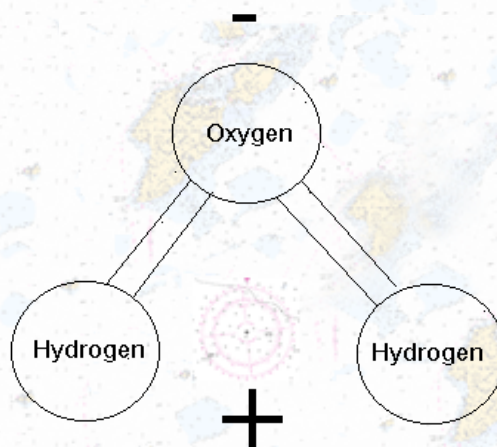


Figure 1. The water molecule, showing positive and negative polarity.

## pH

Pure distilled water is not a homogeneous mixture of  $H_2O$  molecules. Water molecules tend to ionize, that is to separate into  $H^+$  and  $OH^-$  ions, which mix with the water. Normally, there are relatively few of these ions, and it is customary to measure the number of  $H^+$  ions present to get a value known as *pH*. In pure  $H_2O$  at room temperature ( $20^\circ C$ ), there are about 0.0000001 grams of  $H^+$  ions per liter (and an equivalent amount of  $OH^-$  ions). You can see that  $0.0000001 = 1 \times 10^{-7}$ , and, dredging up memories of mathematics long forgotten, you may even recall that the logarithm of this number is the exponent (-7). Make that exponent positive (take the negative exponent) and you have 7, the pH of pure water at room temperature.

*Acids* are substances which decrease the pH of a solution. They work by splitting up water molecules, moving in with the  $OH^-$ , and leaving "orphan"  $H^+$  floating around. *Bases* work the opposite way; they split up the  $H_2O$ , but they combine with the  $H^+$  and leave extra  $OH^-$  in solution. Of course, there are also those acids and bases which affect pH directly; hydrochloric acid (HCl) in  $H_2O$

disassociates to form  $H^+$  and  $Cl^-$ , and sodium hydroxide ( $NaOH$ ) disassociates to form  $Na^+$  and  $OH^-$ . Acids and bases differ in their strength, that is, their ability to change pH.

To measure the effect of an acid or base, all we have to do is measure the  $H^+$  ion concentration of the water. If the addition of a substance to the water increases the  $H^+$  ion concentration, the substance is an acid; if it reduces the  $H^+$  ion concentration, it is a base. Measurement of the  $H^+$  ion concentration usually takes advantage of its electrical properties, and the most accurate determinations of pH are now made with electronic devices known as pH meters which use electrodes to measure the electrical properties of a solution under examination. If the solution has 0.000001 grams of  $H^+$  ions per liter, this corresponds to a pH of 6 (an acidic solution); if there are 0.00000001 gr  $H^+$ /l then the pH is 8 (a basic solution) (Figs. 2,3).

## pH and Hydrogen Ion Concentration

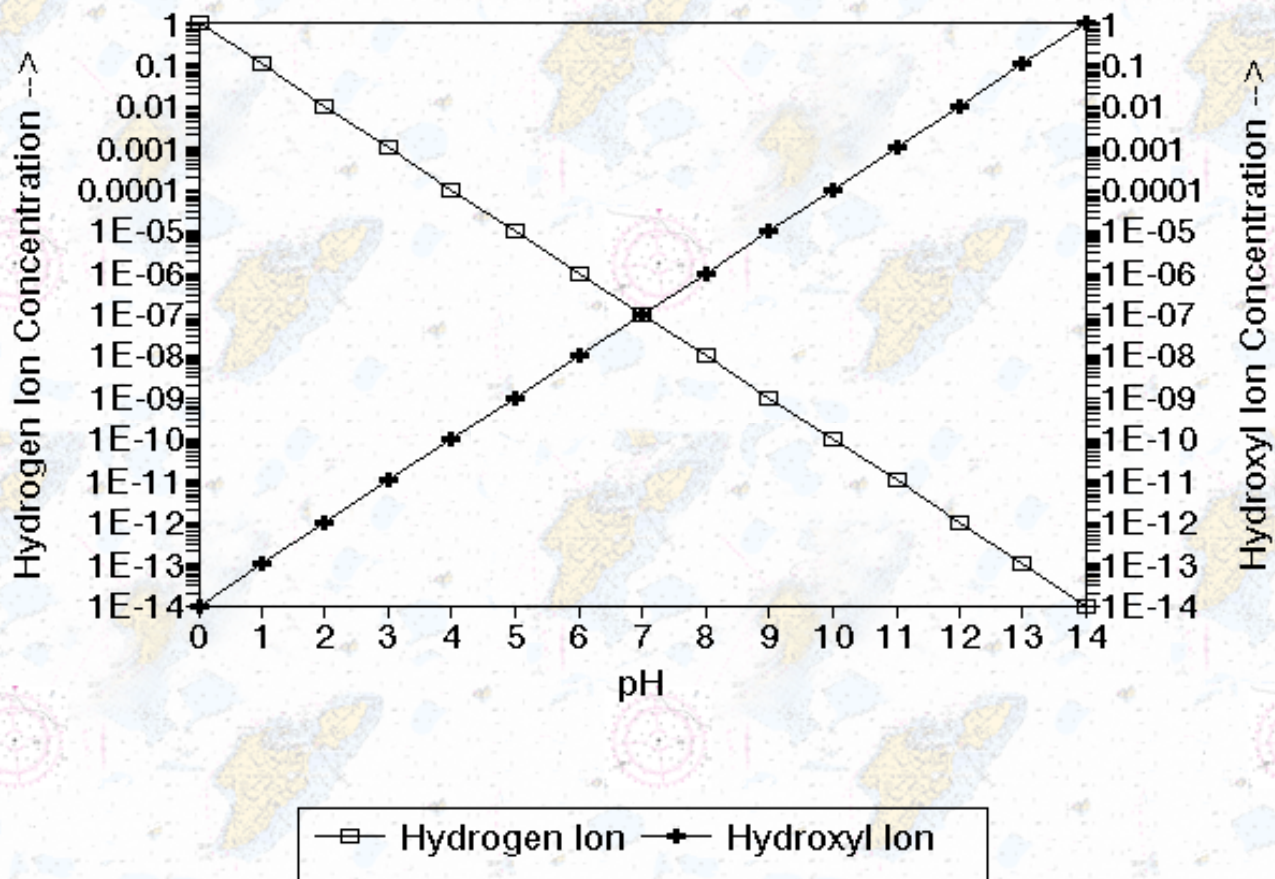


Figure 2. The pH scale, showing concentrations of both  $H^+$  and  $OH^-$  ions. Note that as pH increases, the concentration of  $H^+$  ions decreases. Note also the logarithmic scale.

Note that a change of one pH unit means a tenfold increase or decrease in the number of ions present; a change of two pH units means a hundredfold change in number, and so on. One of the reasons people do not worry about acid rain as much as they should is that they don't realize that small changes in pH numbers mean huge changes in the actual numbers of ions in the water (Fig. 3).

# pH and Hydrogen Ion Concentration

## Normal Scale

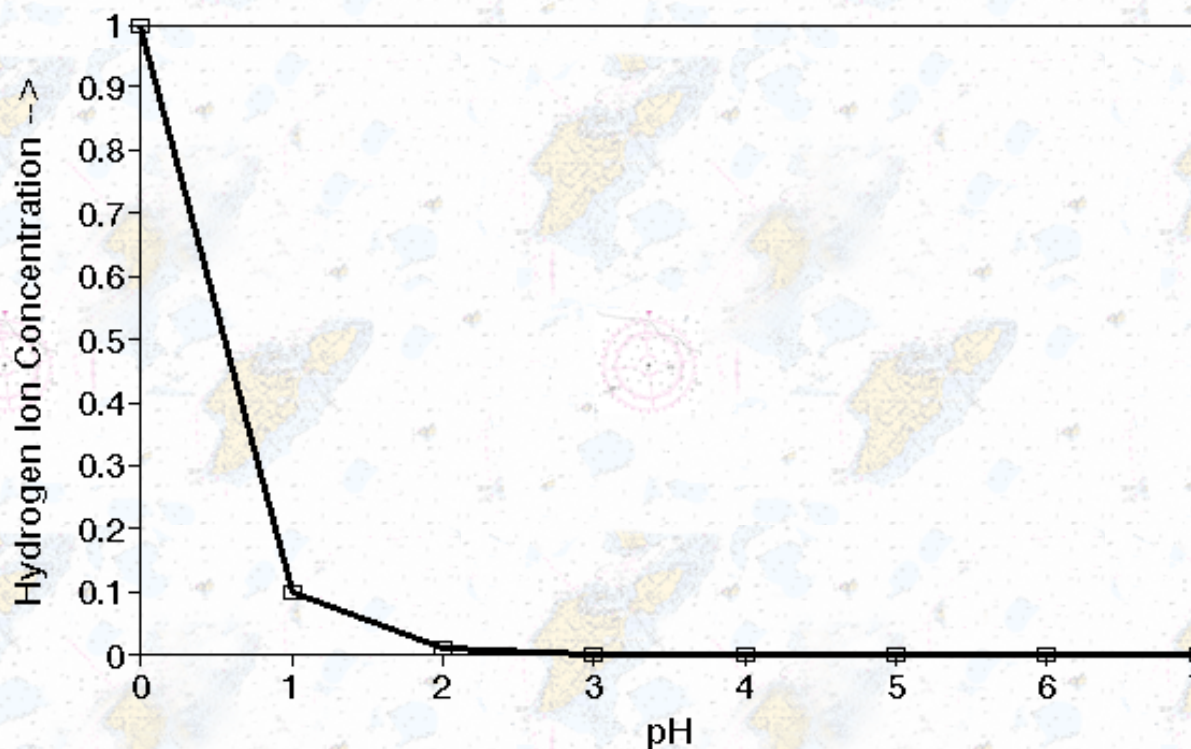


Figure 3. A portion of the pH scale with a natural y-axis; note the dramatic decrease in  $H^+$  ions that occurs with each unit change in pH.

Most organisms operate best when the pH surrounding their cells is about 7, and natural waters usually oblige them. The pH of clean mountain lakes (almost pure water) is usually about 7; the pH of the oceans is about 8. Local conditions can affect pH. Addition of  $CO_2$  to water decreases pH (makes the water acidic); removal of  $CO_2$  makes water basic. Respiration and photosynthesis can therefore have an effect on pH, particularly in areas where water flow is negligible.

*Buffers* are compounds which reduce the effects of acids or bases. The presence of a buffer usually prevents major changes in pH even if a strong acid or base is added to the system. In the human body there are numerous buffer systems to prevent pH changes; these include proteins and inorganic buffers. In natural systems, all of the buffers are inorganic. Sodium bicarbonate ( $NaHCO_3$ ) is one of the major natural buffers; it is abundant in the ocean, and in freshwater where there are limestone rocks (which are largely carbonate deposited from earlier, buffered oceans). Areas such as the Adirondacks, with mostly granite rocks and little limestone, have little buffering capacity and thus are susceptible to pH changes due to acid rain. The "buffers" in things like aspirin (an acid) prevent stomach pH from becoming even more acidic.

The pH of a solution is critical since it changes a number of parameters. Some substances change their solubility or reactivity as pH changes. Proteins may change their shape and thus change their reactivity. Almost anything that dissolves in  $H_2O$  will affect the pH somewhat, and we will consider those effects as we examine those substances.

### Salinity

When water falls to earth, it is chemically pure - well, at least it used to be. In any event, it normally carries relatively few dissolved chemicals. We say that it has a low *salinity*. As it flows towards the oceans, it dissolves more and more molecules of various sorts from the rocks and soil it passes over - a process we call *weathering*. It also picks up materials released from plants and animals, either as waste products or through decay of their bodies. Since water does not leave the oceans except by evaporation (which removes only water, leaving the other materials behind), these materials accumulate in the oceans, and the oceans have a salinity much greater than that of freshwater. In turn, the salinity of freshwater increases as it flows to the oceans, and coastal areas such as *estuaries* may have a salinity reflecting the mixture of fresh and salt water. Other areas that allow water to leave only by evaporation also may have salt water. For instance, if you do not periodically allow water to flow completely through your houseplant pots, or if you never remove water from your freshwater aquarium, they will become salty.

We call it salt water because most of the dissolved substances are just that - salts, simple ionic compounds that typically disassociate completely into positive and negative ions in water. Since an equal number of positive and negative ions are added in

such cases, most salts do not change the pH appreciably, unless one of the components happens to be  $H^+$  or  $OH^-$ . Note, however, that the presence of salts may affect the chemistry of certain pH tests, which may only be accurate when used in either fresh or salt water (some chemical tests will work in both). The most abundant of the salts found in the oceans is NaCl, sodium chloride or table salt. We measure salinity in terms of the number of grams of dissolved salts in 1000 g (one l) of seawater. Since all these salts affect the electrical conductivity of the water, it is simple to measure salinity with an electrical meter. The more current that passes through a solution, the greater its salinity. Seawater ranges in salinity, but a useful approximation is 35 g / kg; or 35 parts per thousand or 3.5%. Places like the Great Salt Lake, certain tidal pools, etc., can have higher salinities; most freshwater systems have dramatically lower salinities.

In seawater, the ions are dominated by  $Cl^-$  (19.353 gr/kg),  $Na^+$  (10.76 gr/kg),  $SO_4^{2-}$  (2.712 gr/kg),  $Mg^{+2}$  (1.294 gr/kg),  $Ca^{+2}$  (0.413 gr/kg),  $K^+$  (0.387 gr/kg),  $HCO_3^-$  (0.142 gr/kg),  $Br^-$  (0.067 gr/kg), and  $Sr^{+2}$  (0.008 gr/kg); other ions are present in trace amounts, including gold. Freshwater is dominated by similar ions, but the amounts are highly variable and depend on season, amount of rainfall, type of rocks, etc. Freshwater with an abundance of calcium and magnesium is termed *hard*; it resists forming suds when detergents are added and leaves a residue. Water softening agents often attempt to chelate these ions out of solution.

The salinity of water is important to organisms for two main reasons: osmoticity and density. We have already considered density; remember that salt water is more dense than freshwater, thus, it is easier to float in salt water. This also means that freshwater flowing into the ocean tends to remain on the surface for some time, and, further, that it takes some energy (tides, wind, currents) to get the two to mix effectively. It is not uncommon in estuaries for freshwater to lie on top of saltwater in layers. Temperature still plays a role; warm freshwater is very likely to lay on top of cold seawater, but other possibilities may also occur, such as warm seawater laying on top of a layer of cold freshwater. We will take up the concept of osmoticity next.

### Osmotic Relations

Imagine water of two different salinities. We say that the more saline solution is *hypertonic* (or hyperosmotic) in relation to the other, or that the less saline solution is *hypotonic* (or hypoosmotic) in relation to the other. If the salinities were the same, they would be *isotonic* (isosmotic). Osmoticity, then, is simply a comparison of the salinities (or, more accurately, the number of dissolved particles, including non-ionic compounds) of two solutions. It is important to remember that, in considering osmoticity, that you must have two different solutions to compare - it is a relative term.

If you mix the two solutions, they will achieve an intermediate salinity. The process of *diffusion* means that all of the ions will, as a result of random chance, distribute themselves evenly throughout the solution. This occurs because the molecules and ions are in constant motion (except at 0 K); diffusion occurs more rapidly at higher temperatures. Stirring, mixing, bulk flow due to density differences (as a result of temperature or salinity) etc., will all decrease the time it takes for the solutions to come into equilibrium, with the dissolved material equally distributed.

Now, place the two solutions in contact with each other, but separated by a membrane. The membrane will have the property of allowing only small, uncharged (polar is OK too) molecules to pass through. Say the one solution is in a sack made of the membrane, and the sack is dropped into the other solution. Will diffusion take place?

The answer is yes and no. Water molecules, being small and (relatively) uncharged, pass through easily, and in both directions. Ions get stopped at the border due to their charge, as do larger molecules such as sugars and proteins, regardless of their charges. For physical reasons we need not get into here, the water molecules will, on average, tend to go more to the hyperosmotic side of the membrane, although a few rugged individualists will still cross over from the hypertonic side to the hypotonic side. The *net* flow of water will be to the hypertonic side. If the outside solution is hypertonic, water will flow out of the sack and the sack will shrink; if the outside solution is hypotonic, water will flow into the bag and it will swell and (perhaps) burst. We have just built a model of a cell (Fig. 4)(ions can penetrate the membrane of a cell, however).

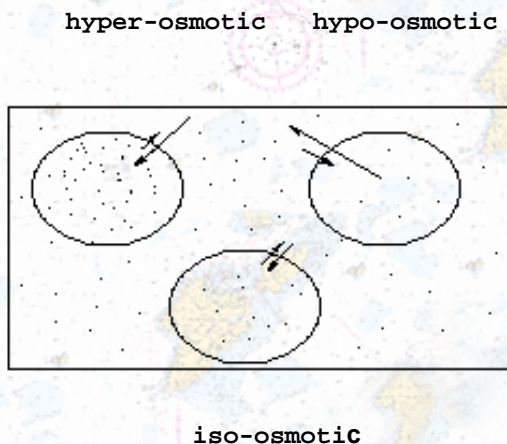


Figure 4. Diagrams of three hypothetical cells of varying osmoticity in relation to the surrounding medium. The dots indicate osmotic particles, the length of the arrows represents relative water flow in the direction of the arrow.

All organisms are faced with the basic problem of maintaining a proper amount of water in their cells. There are two solutions; one is elegant in the extreme - allow water to move into or out of the cell as it pleases, and waste no energy on correcting it. This strategy is

known as osmoconformation, and works only if the organism is in an unchanging environment - like the middle of the ocean, or deep inside a body. It is no accident that the salinity (though not the precise ionic makeup) of our cells - and the cells of most living things - is isotonic with seawater.

Moving into freshwater (or moving onto land) requires a different strategy. Freshwater is simply too dilute to keep life in a cell going. You need more stuff in your cells, and that stuff increases tonicity. Freshwater organisms face a constant influx of water from the surrounding hypotonic medium, and they can potentially lose important ions to that solution also. Therefore, the strategy among most freshwater organisms is to cover as much of the body as possible with an impermeable coat, and leave all water exchange to a relatively small number of cells. These cells will maintain the water balance, and the remaining cells are bathed in an isotonic solution. Cells can maintain osmotic balance by using ATP to actively pump  $\text{Cl}^-$  ions into the cell. The inside of the cell becomes negatively charged, and other ions, such as  $\text{Na}^+$  come in because of this. Water that flows in is passed on to the blood and excreted as a dilute urine (Fig. 5).

## Osmotic Regulation in Fresh and Salt Water

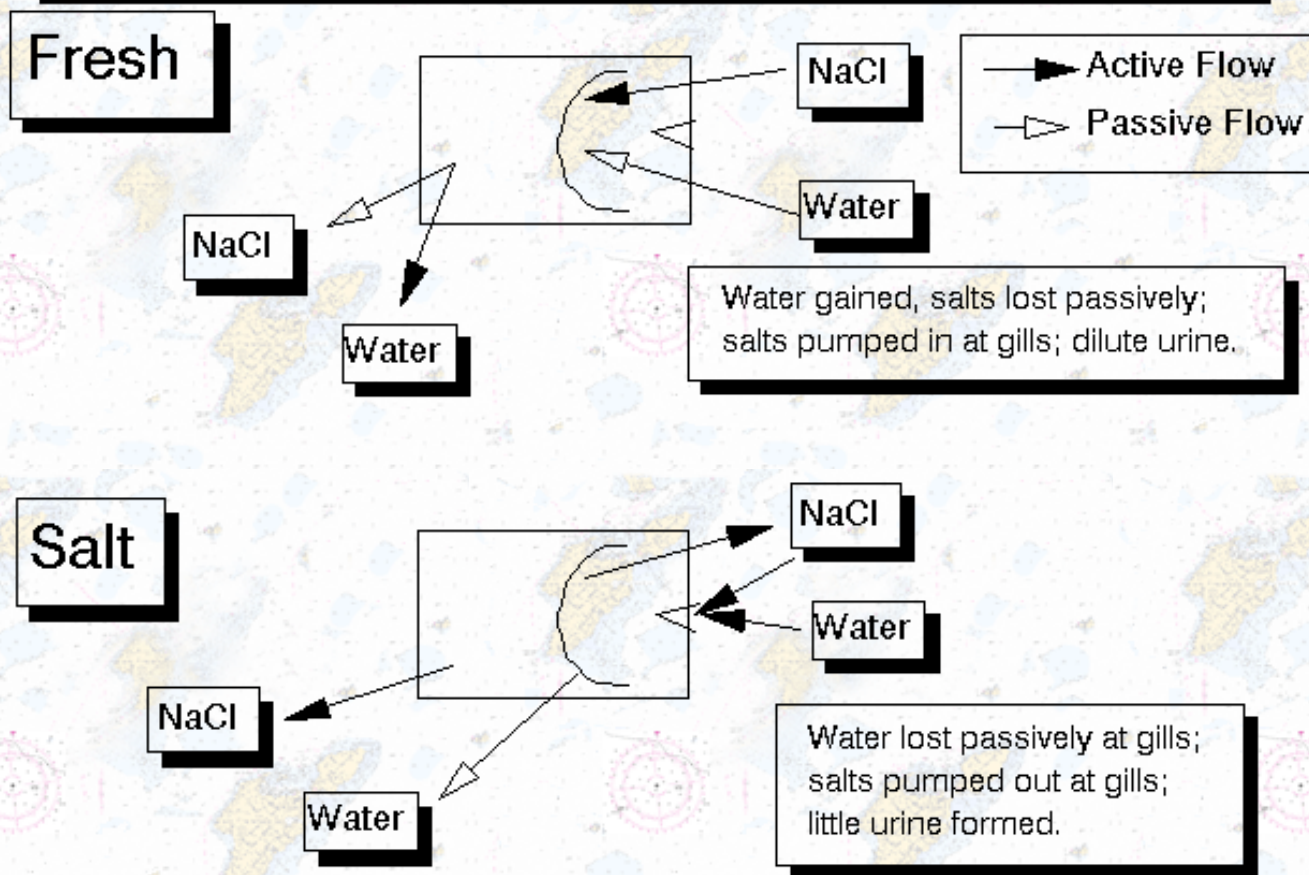


Figure 5. Diagrams of two hypothetical "fish", one in freshwater and one in saltwater. Main sites of ion exchange are the gills and the excretory organs (kidneys).

Osmotic exchange also takes place across the lining of the gut (not shown here). The freshwater fish gains water but loses ions passively across the gills; to compensate, the gills actively pump in ions and the kidneys form a dilute urine. The saltwater fish gains ions and loses water across the gills; to compensate, water is ingested (along with salt), the gills actively pump ions out of the body, and a small amount of relatively concentrated urine is formed.

Many marine organisms (those which maintain their internal fluids hypotonic to seawater, perhaps reflecting the salinity of the sea when they evolved), and all terrestrial organisms, face the problem of water loss. This is conquered in reverse fashion. These organisms drink seawater, absorb water (and ions) from the gut, and pump ions out through specialized cells.

The specialized cells in marine organisms are the same as those used by freshwater organisms to pump ions in; it's just that the membrane-bound proteins which form the ion "pumps" are "installed" backwards. These  $\text{Cl}^-$  pumping cells, whichever way they pump, are called *chloride cells*. In fish (both freshwater and marine), they are located on the gills. Because respiratory structures must have relatively permeable surfaces for gas exchange, they are also a common place to put chloride cells on a body which is otherwise impervious to water flow. Another popular place is in the gut and kidneys, in both places ion concentrations are manipulated to get water to flow where the organism wants it to.

### Dissolved Gasses

The atmosphere is about 78% nitrogen, 21% oxygen, and only 0.033% carbon dioxide (but we're working on that). These three gasses have different solubilities in  $\text{H}_2\text{O}$ , however. To measure solubility, imagine this experiment: Replace all the air in the

atmosphere with only the gas you are interested in so that at ground level the pressure is 1 atmosphere. If you now take one liter of water (let's say at 10° C), it will become saturated with the gas. In our imaginary world, if the gas was nitrogen, the water would hold 18.61 ml of it; if the gas was oxygen, the water would hold 38.46 ml of it; if the gas was carbon dioxide, the water would hold a whopping 1,194 ml of it! If you're wondering how 1 liter of water can hold 1.194 liters of gas, get a liter of Perrier and shake it up - then open it. The solubility experiment tells us that oxygen is about twice as soluble as nitrogen, and that CO<sub>2</sub> is about 1,000 times more soluble than either nitrogen or oxygen. Of course, in the real world there is not 1 atmosphere of pressure of each of these gasses, each gas has a *partial pressure* corresponding to the percentage of the atmosphere that it makes up. Multiplying the solubility of the gas by its percentage in the atmosphere gives the amount of that gas that will be dissolved in the water:

### Solubility of Gasses in H<sub>2</sub>O at 10° C

Gas	Percent	Solubility*	In water*
Nitrogen	78.084%	18.61	14.53
Oxygen	20.946%	38.46	8.06
Carbon Dioxide	0.033%	1,194.00	0.39

\* Solubility in ml/l

The absolute amount of a gas in water solution will vary with several factors. Increasing temperature will reduce the amount of gas that water can hold; you are familiar with this fact already, since it is manifested whenever you heat water (the small bubbles that form before the water boils). Decreasing pressure (increased altitude) will also decrease the amount of gas dissolved. Increasing salinity also decreases the ability of water to dissolve gasses; seawater holds about 20% less gas than freshwater, and hypersaline water holds even less gas. And, of course, there are other gasses which are dissolved in water besides these three (which are the major ones).

#### Oxygen:

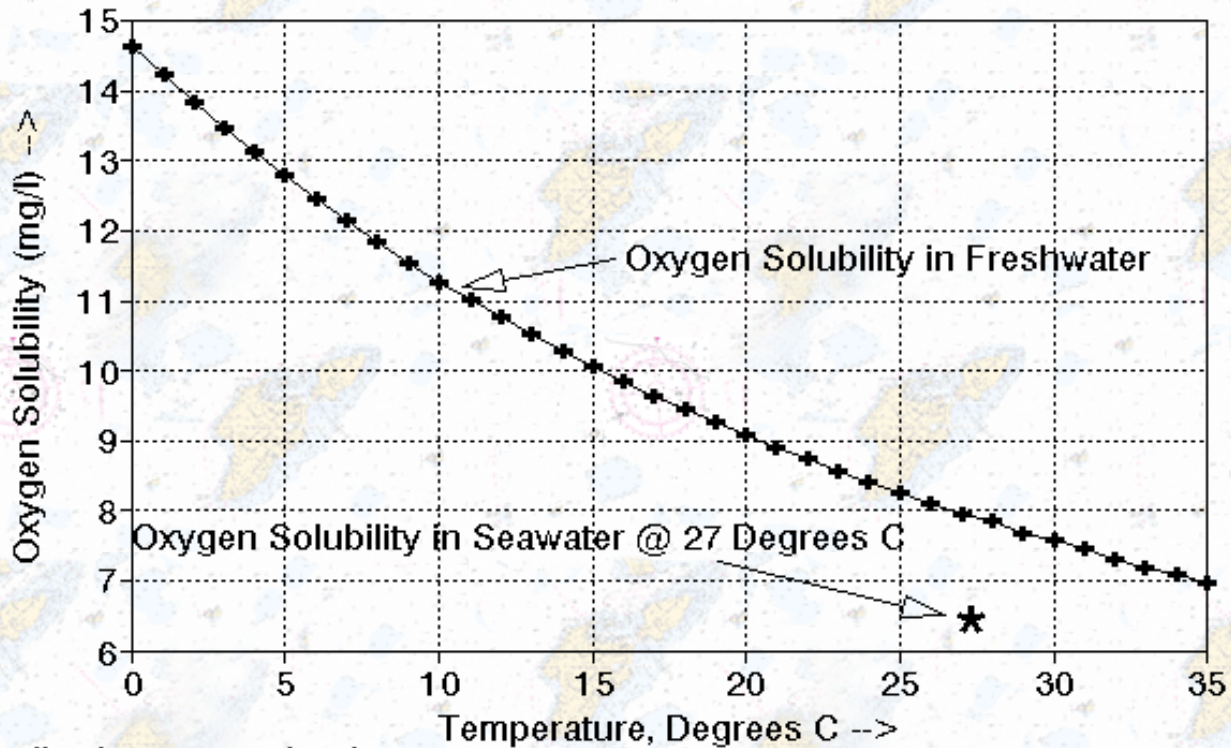
Oxygen, of course, is of critical importance to living organisms. It is important to remember that oxygen is a potent poison, and that too much can be a bad thing. We're probably lucky that the atmosphere has only 21% O<sub>2</sub>; astronomers on other planets have probably concluded that life cannot exist on Earth because of the high levels of noxious oxygen. Any more O<sub>2</sub> and it would probably start to poison the process of photosynthesis (actually, it already does to a point, the reaction is called photorespiration). In water, however, it is easy for O<sub>2</sub> concentrations to become depleted in local areas, such as in sediments or the bottom of stagnant bodies of water. These local areas of oxygen depletion serve as important refugia for the many ecologically significant anaerobic organisms, and thus should not be viewed automatically as "bad". Nitrogen fixation, for instance, is notoriously sensitive to O<sub>2</sub>; root nodules of legumes and heterocysts of Cyanobacteria are structures built to exclude O<sub>2</sub> so that nitrogen fixation can take place.

The solubility of O<sub>2</sub> in water is slightly more complex than was explained initially above. Better estimates of O<sub>2</sub> solubility involve moist air as opposed to the dry air in our theoretical planet experiment. Oxygen solubility is also very temperature dependent. In general, the solubility of oxygen can be estimated by the equation:

$$\text{solubility (mg/l)} = \frac{468}{31.6 + t}$$

Where t is degrees C; note that we are now talking about milligrams, not milliliters. Thus, for a t of 10° C, there should be 11.25 mg O<sub>2</sub>/l; at 20° C there should be 9.069 mg O<sub>2</sub>/l; and at 0° C there should be 14.81 mg O<sub>2</sub>/l at saturation (Fig. 6). These values are for sea level and fresh water; at altitude or in salt water the saturation values would be lower. Water is not always at saturation, however. Organisms within the water can quickly use up dissolved O<sub>2</sub>, and replacement by diffusion may not equal the rate of respiration, thus resulting in lower O<sub>2</sub> levels. Oxygen enters the water through diffusion from the atmosphere and from photosynthesis. Diffusion from the atmosphere may be enhanced by any type of turbulence such as water flowing over rocks, waves, wind, etc.; photosynthesis is dependent on many factors. Oxygen loss is primarily due to respiration of animals and plants in the water; respiration is temperature dependent, with more respiration occurring at higher temperatures.

# Oxygen Solubility in Fresh Water as a function of temperature



- all values at sea level -

Figure 6. Oxygen solubility at saturation for fresh water at sea level at various temperatures.  $O_2$  solubility decreases with increasing temperature, note also the single point plotted for salt water; salinity significantly decreases the amount of  $O_2$  in solution.

These relationships set the stage for determining the critical factors for  $O_2$  availability in water. More oxygen will be available in cool, sunny, turbulent habitats (uptake of  $O_2$  by organisms is also enhanced by flow or turbulence since more water will pass over respiratory structures per unit time). Oxygen will be in short supply under warm, dark, stagnant conditions, where respiration is high and no photosynthesis is taking place. In natural aquatic systems,  $O_2$  stress most often occurs at the water-sediment interface on dark, calm nights in the middle of the summer or dry season, when water flow is at a minimum. Any pollutant which adds to the amount of plant life present (fertilizers), or which contributes organic matter which will be decomposed by aerobic bacteria (sewage), will aggravate the  $O_2$  stress at that time. Also in natural systems, the most  $O_2$  is available in cool habitats with shallow water, particularly in turbulent headwater streams or near wave-swept coasts.

Oxygen concentration in the water can be measured by either electrical meters or by chemical methods. The meters use electrodes and must be calibrated or adjusted to compensate for temperature (most include an electrical thermometer attached to the probe), altitude, and salinity. Chemical tests, such as the well-known *Winkler Method*, which measures oxygen by determining how much of a standard chemical is oxidized, work by titration. Results are often expressed in *percent saturation*; for instance, if the water is at 20°C and measures 8 mg  $O_2$ /l rather than the saturation value of 9.069 mg  $O_2$ /l, the percent saturation would be 88%. It is not unknown to have *supersaturated* water; this results in percent saturations over 100%, under such conditions  $O_2$  is released to the atmosphere - which is how it got there in the first place!

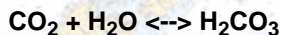
Another important concept to consider is Biochemical Oxygen Demand, or *BOD*. *BOD* is the measure of how much oxygen is taken up from the water by both biological agents (organisms) and simple chemical reactions (like  $Fe + O_2 = rust$ ). To measure *BOD*, a sample of the water (and/or sediment) is measured for  $O_2$  content, sealed up, and left for a specified period (often 24 hours). The  $O_2$  level is measured again, and the amount of  $O_2$  used up (mg), or the rate of  $O_2$  use (mg/hour) is reported as the *BOD*. Regulations governing sewage plants, stockyards, etc., may specify the amount of *BOD* that can be released each day.

## Carbon Dioxide:

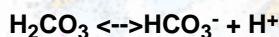
Carbon dioxide is ying to oxygen's yang. As one is evolved in respiration or photosynthesis, the other is taken up. Still, the much

greater solubility of CO<sub>2</sub> compared to O<sub>2</sub> means that the relationship of CO<sub>2</sub> to water is much different compared to that of O<sub>2</sub> and water. For one, CO<sub>2</sub> dissolved in H<sub>2</sub>O increases acidity. Secondly, CO<sub>2</sub> can combine with other chemicals in the water to form different compounds; these compounds further affect the chemistry of the water. The primary sources of CO<sub>2</sub> in water are biological (respiration), geologic (weathering of carbonate containing rock such as limestone) and from the atmosphere. Rainwater in particular, with its high surface area, picks up a lot of CO<sub>2</sub> as it falls.

A small amount of CO<sub>2</sub> entering water combines with the water to form carbonic acid:



The carbonic acid, in turn, may dissociate:



The HCO<sub>3</sub><sup>-</sup> is known as *bicarbonate*, and may be taken up by photosynthesizing plants. Changing the pH of a solution changes the relative concentration of the various CO<sub>2</sub> forms; a decrease in pH (more acid) leads to more CO<sub>2</sub> and H<sub>2</sub>CO<sub>3</sub>; an increase in pH (more basic) leads to an increase of the CO<sub>3</sub><sup>-2</sup> ion. In order to measure the amount of CO<sub>2</sub> present, one must obviously know the pH of the solution.

Carbon dioxide may also combine with water and metals such as magnesium and calcium to form other bicarbonates. The amount of CO<sub>2</sub> so combined is referred to as *alkalinity*, which really has nothing to do with OH<sup>-</sup> concentration, but much to do with the buffering capacity of the water. It works like this: Highly alkaline water tends to have a high (basic) pH and will turn a phenolphthalein solution pink. If you add acid to it, the bicarbonates, with their negative charge, attract and bind the positive H<sup>+</sup> ions, and form carbonic acid. If you keep adding acid, eventually the pH changes to 8.3, and the pink fades. The amount of acid added corresponds to the *phenolphthalein alkalinity*, but not all the bicarbonate is converted at this point; in fact, it is at its peak. If you now add methyl orange, a dye that will change color at pH 4.4, and continue to add acid, you will drive more bicarbonate to form carbonic acid, which in turn reaches its peak at a pH of 4.4. The total amount of acid added thus corresponds to the amount of CO<sub>2</sub> present in the sample. This method works only if there are not significant numbers of non-carbonate negative ions to absorb H<sup>+</sup> ions.

Testing for CO<sub>2</sub> is usually done chemically, and is quite complicated. It is based on the above reactions and works *something* like this: if phenolphthalein added to a water solution turns pink, then the pH is over 8.3 and significant bicarbonates, including those of Ca<sup>++</sup> and Mg<sup>++</sup>, are present. The solution is titrated with acid to a pH of 4.4, and the total amount of acid added corresponds to the amount of CO<sub>2</sub> present (as bicarbonate). If the initial solution with phenolphthalein does not turn pink, then a lesser amount of CO<sub>2</sub> (as bicarbonate or whatever) is present, and bicarbonate is titrated until a pink color appears. The amount of bicarbonate added will then correspond inversely to the amount of CO<sub>2</sub> that was present initially; the more bicarbonate you have to add, the less was there to start with.

An interesting reaction may take place when CO<sub>2</sub> is removed from water during photosynthesis - a precipitate of CaCO<sub>3</sub> (calcium carbonate) may form. This reaction, along with calcium carbonate formation by corals, has led to the production of most of the limestone in the world. Weathering of that limestone, in turn, yields much of the carbonate present in freshwaters, and, as we have seen, that carbonate forms an effective buffer against decreased pH due to acid rain. As a result of the many forms it can take, CO<sub>2</sub> is usually present in ample amounts for photosynthesis to occur in aquatic habitats. Although rarely a limiting factor, it is known that more alkaline lakes are, up to a point, more productive than less alkaline lakes. However, as we shall soon see, other factors, such as the abundance of phosphorous and nitrogen, are more often limiting factors, and levels of these plant nutrients are usually correlated with alkalinity, making the independent factors hard to sort out.

### Plant Nutrients - Nitrogen and Phosphorous

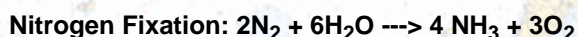
Aside from O<sub>2</sub> and CO<sub>2</sub>, there are a variety of other chemicals needed by living things. Animals, almost by definition, obtain these other chemicals along with the carbohydrates and proteins they ingest when they consume other animals or plants, therefore, animals are usually content as long as the water has enough O<sub>2</sub> and a decent salinity. Plants, on the other hand, are more self-sufficient, and they can synthesize a wide variety of complex molecules from simple inorganic precursors. The ecological community that will develop in a body of water is thus often dependent on the suitability of the habitat for the growth of photosynthetic organisms. Exceptions to this include the deep ocean (which is dependent, however, on the growth of phytoplankton above), or headwater streams (which depend on adjacent trees for most of their organic input through leaf fall), or cave streams (bat guano) and so on.

Along with sunlight and CO<sub>2</sub>, the major needs of a plant include macronutrients nitrogen and phosphorous (used for proteins, DNA, RNA, ATP, etc.) and micronutrients such as sulfur (protein), magnesium (chlorophyll), and iron (cytochromes) (this list is not comprehensive). The micronutrients may be found in very small concentrations; plants (I will use the term plants to refer to all photosynthetic organisms) are good at obtaining them even if they are in low concentration; and they are rarely a limiting factor (be sure to review your ecology to be sure that you understand the concept of limiting factor). Some micronutrients, such as sulfur (as SO<sub>4</sub><sup>-2</sup>), magnesium (as Mg<sup>+2</sup>), calcium (as Ca<sup>+2</sup>) and potassium (as K<sup>+</sup>) are important constituents of both seawater and freshwater, as we have seen earlier.

Phosphorous (P) and nitrogen (N) are critical to plant growth, and they (usually P, but sometimes N) are often limiting factors to

plant growth. Before you object, recalling that dissolved nitrogen is common in water, remember that it is dissolved nitrogen gas,  $N_2$ , which is inert and cannot be used by most plants. The exception here are the cyanobacteria, which can fix  $N_2$  in the heterocysts, which provide a local anoxic environment for the nitrogen-fixing enzymes (and bacteria in anoxic root nodules of legumes and other anoxic places in the soil). Bodies of water with a low N/P ratio are thus prone to blooms of cyanobacteria. For most plants, N must be in the form of nitrate ( $NO_3^-$ ) or ammonia ( $NH_3$ ,  $NH_4^+$  in water). Ammonia, of course, is the nitrogenous waste of choice for many aquatic organisms, and even more is released by bacteria breaking down dead plants and animals or other nitrogenous animal wastes such as urea. Nitrate is a product of the nitrogen cycle; the nitrogen cycle in water differs slightly from the nitrogen cycle that takes place on land (which you are probably familiar with).

On land,  $N_2$  is fixed by bacteria in the soil such as *Rhizobium*, *Clostridium*, and *Azotobacter*; in the water (both freshwater and marine)  $N_2$  is fixed by such cyanobacteria as *Anabaena*, *Plectonema*, and *Nostoc*. The reaction requires energy and proceeds as follows:

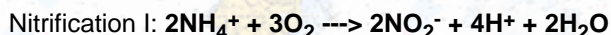


Ammonia, whether generated by nitrogen fixation or by the breakdown of amino acids by animals or decomposers, is toxic. As the pH of water increases, more of the ammonia exists in the water as  $NH_4^+$ .  $NH_4^+$  is even more toxic than  $NH_3$ , and the fact that it is more prevalent at higher pH leads to one of the significant differences between keeping a marine and a freshwater aquarium. A marine aquarium typically has a pH of 8.0 to 8.5; a freshwater aquarium will usually have a pH of about 7. At pH 8.0, there is far more  $NH_4^+$  present, and, if too many animals are producing too much  $NH_3$ , then  $NH_4^+$  levels will soon become toxic. Therefore, marine tanks must be "aged", that is, stocked slowly, to allow populations of bacteria to develop to remove the ammonia. The role of these latter bacteria will be explored below.

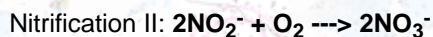
Once produced, ammonia ( $NH_3$ ) is used by a variety of plants and bacteria as the source of the amino group for amino acid synthesis (another reason that freshwater tanks are more tolerant than marine tanks in regards to ammonia is the ready availability of freshwater plants which help reduce ammonia levels). The amino acid synthesis reaction also requires energy and looks like this:



Note that both this reaction and the preceding one release  $O_2$  into the atmosphere; photosynthesis is not the only source of  $O_2$  in the atmosphere! While amino acid synthesis does remove some ammonia from the water, much more is usually present. Another reaction, *nitrification*, takes ammonia and converts it to *nitrite* ( $NO_2^-$ ); this reaction releases energy to the organism which carries it out:



In water, this reaction is carried out mostly by bacteria of the genus *Nitrosomonas*. Nitrite is less toxic than ammonia, but is still toxic; high levels of nitrite can kill many aquatic organisms. Fortunately, a further nitrification reaction can occur (also with a release of energy):



The end product here, *nitrate* ( $NO_3^-$ ), is even less toxic than nitrite, and can be used by many plants as a nitrogen source. In aquatic systems and terrestrial systems as well, this reaction is carried out by bacteria of the genus *Nitrobacter*. In a typical marine aquarium, nitrate may approach toxic levels, but this process takes months. In addition, a number of *denitrification* reactions take place and reduce nitrate levels, as does uptake by plants.

To retrace the nitrogen cycle, let us consider the marine aquarium again (Fig. 7). Ammonia levels build as animals excrete nitrogenous wastes; as they die and decompose; as food (with protein) is added; and as  $N_2$  from the atmosphere is fixed by cyanobacteria. Because of the high pH (8.0), most of the ammonia will exist as toxic  $NH_4^+$ . *Nitrosomonas* bacteria will convert the ammonia to nitrite, and *Nitrobacter* bacteria will convert the nitrite to nitrate, which can be utilized by plants. Denitrification will remove some of the nitrate from the water. In a freshly established marine tank with a few fish, it is not uncommon for the ammonia levels to peak, then drop as the *Nitrosomonas* bacteria take hold and begin to convert ammonia to nitrite. As nitrite levels build and peak, *Nitrobacter* populations will thrive and convert the nitrite to nitrate, reducing nitrite concentrations to near zero. Typically, it takes about one month for the bacterial populations to become established, and it is usually wise to monitor the process by daily tests of ammonia and nitrite levels. The number of organisms that can be maintained in a marine tank is usually proportional to the amount of surface area on the gravel of the aquarium available for the *Nitrosomonas* and *Nitrobacter* bacteria to attach to.

## The Nitrogen Cycle in Water

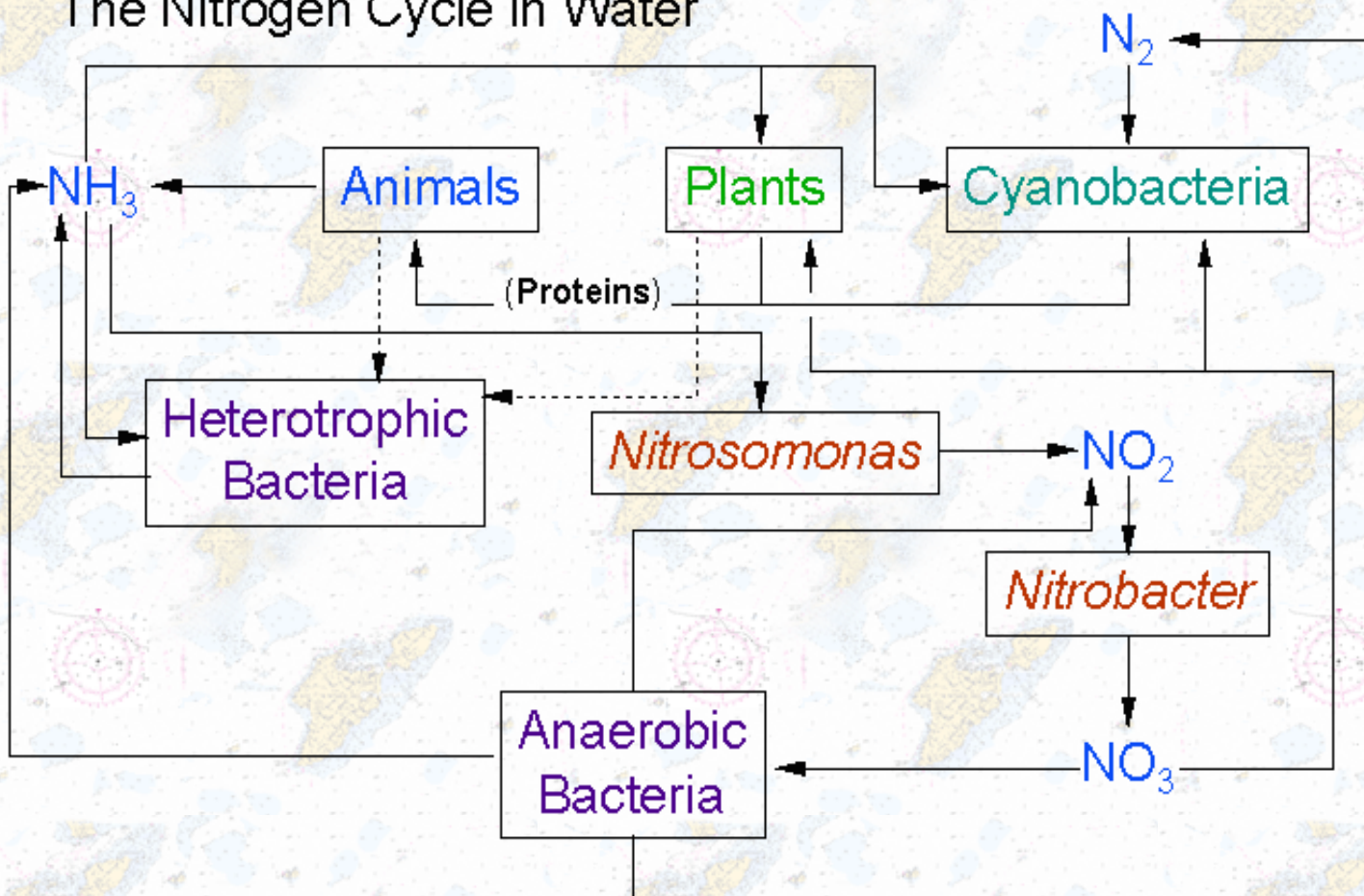


Figure 7. Diagram of the Nitrogen Cycle in water.  $N_2$  in the air is fixed by cyanobacteria and put in the form of protein, which is eaten by fish. Fish release  $NH_3$ , which is taken up by heterotrophic bacteria, plants, cyanobacteria, and the bacterium *Nitrosomonas*. The first three reincorporate the  $NH_3$  into protein, *Nitrosomonas* converts it to  $NO_2$ , which is taken up in turn by *Nitrobacter*, which gives off  $NO_3$ . The  $NO_3$  is a plant nutrient and is also utilized by anaerobic bacteria, which can produce  $N_2$ ,  $NO_2$ , or  $NH_3$ .

The story with phosphorous is much simpler. Phosphorus is typically available to plants as *organophosphate* ( $PO_4^{-3}$ ); this compound is a common weathering product of igneous rock. Other sources of phosphate are decaying animal bodies, animal wastes, bones of vertebrates, and bird guano. The last is mentioned specifically because it is such a rich source of phosphorous; in fact, huge quantities of bird guano that accumulate near nesting areas of shorebirds are often mined for fertilizer. Phosphorous trapped in the bodies of dead organisms which sink to the bottom may accumulate in bottom sediments; this phosphorous will become available again to living plants (animals do not take up phosphorous directly from the environment) when currents sweep the bottom and bring it to the surface where there is sufficient light for photosynthesis (remember the LCP?). In nature, two such currents are noteworthy, the *overtum* of lakes (which occurs when the water is all of the same temperature and density, more on this later), and *upwellings*, places where cold ocean currents meet continents and rise up from the bottom. The most famous example of an upwelling is off the coast of Peru; as the cold water reaches the surface (replacing warm surface waters blown west by prevailing winds), it brings up phosphorous, which encourages the growth of abundant algae, which in turn are appetizers for anchovies, which are then fished in great numbers by humans (for pizza topping) and birds (where do you think the guano comes from?).

Phosphorous is often the limiting factor for plant growth in aquatic systems. In many aquatic habitats, it is impossible to measure any free phosphate in the water when heavy algal growth (blooms) are in progress, mostly because the algae use up the phosphate as soon as it becomes available. Many algae store inclusions of phosphorous (when available) in their cells as a "hedge" against later phosphate shortages. Tremendous algal blooms are a symptom of *eutrophication*, a natural process that occurs as lakes age and accumulate phosphorous. Such huge blooms of algae can cause problems when they die and decompose, or when, particularly on hot, still summer nights, their respiration uses up all the  $O_2$  in the water.

Many human activities accelerate the process of eutrophication; this leads to a phenomenon known as *cultural eutrophication* to set it apart from the natural process. In cultural eutrophication, phosphorous from agricultural runoff (phosphate fertilizers, animal wastes), human sewage, detergents, etc., is added to the water. The much publicized "death" of the Great Lakes was (is) due to cultural eutrophication. A eutrophied lake is typified by heavy algal growth, turbid water, and overall high productivity. The opposite, an *oligotrophic* lake, has clear water with little life (paradoxically, highly eutrophic lakes such as our "dead" Great Lakes, are teeming

with life, while pristine oligotrophic lakes are nearly sterile). Remedies to cultural eutrophication include soil erosion control (much phosphorus is carried into aquatic systems bound to soil particles), careful use of fertilizers (the use of fertilizers on grass is criminal and should be totally banned), and *tertiary* sewage treatment (primary treatment kills germs, secondary removes solids, tertiary removes phosphorus and other chemicals). Even after the source of phosphorus is found and diverted, the sediments may contain enough phosphorus to keep the lake eutrophic for years. Again, under natural conditions, oligotrophic lakes occur near headwaters where little weathering has occurred to release phosphorus, and eutrophic lakes are found downstream (downstream is usually geologically older), where phosphorus inputs from the upstream sites make abundant algal growth possible.

**Further Reading:**

Forsberg, Curta. 1998. [Which policies can stop large scale eutrophication?](#) Water Science and Technology. Vol: 37, Issue: 3, pp. 193-200

Cole, G.A. 1983. *Textbook of Limnology*. 3rd. Ed. Waveland Press, Prospect Hts., IL, 401pp. [Read Chapters 11-14](#)

McCafferty, W.P. 1981. *Aquatic Entomology*. Science Books Intl., Boston. 448 pp.

Mowka, E.J., Jr. 1979. *The Instant Ocean Handbook*. Aquarium Systems Inc. 20pp. [Read](#)

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## Aquatic Habitats

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When considering aquatic habitats, many variables come to mind. Obviously, there is a continuum of salinity ranging from essentially distilled water at glacier faces and high mountain streams, to other freshwaters, to estuaries where fresh and salt waters mix, to oceans, to hypersaline environments such as the Great Salt Lake. Current is another factor; water may be still and stagnant, or flow in currents of various velocities. Currents may be unidirectional, such as in streams, or multidirectional, such as when waves wash across a beach. Aquatic habitats may occur in open water, or they may be associated with the bottom of the body of water, and both will be affected by the mechanical and chemical makeup of the local geology. All sorts of daily and seasonal temperature regimes can be expected. Aquatic habitats vary in the amount of light they receive and range in size from tiny pools at the base of a plant to the Pacific Ocean in size.

## *Freshwater vs. Marine Habitats*

The obvious difference when comparing these two extremes is the salinity of the water, and the differences associated with that salinity. One obvious consequence of the difference in salinity is the change in osmoregulatory strategy that must take place. Many organisms in salt water are osmoconformers, essentially isotonic in relation to the seawater, although they may regulate certain ions at levels different from those of the surrounding ocean. A fair number of marine organisms are hypotonic in relation to the seawater and must therefore actively take up water to replace that they lose to the seawater. Of course, in taking on that water, they usually take in too many ions, and they must have some mechanisms for expelling those ions.

Organisms in freshwater have the reverse problem. They tend to take on water from the environment, and, in expelling the excess water, may lose important ions. Since freshwater is too dilute to make a good cytoplasm, it is no surprise that all freshwater organisms are hypertonic to the environment and that in consequence they must be active osmoregulators. Most have some mechanism to pump ions into the body. Of course, the whole problem of osmoregulation can largely be avoided by an impermeable outer body; but this in turn makes  $O_2$  uptake from the surrounding medium impossible. The respiratory surfaces thus become major sites of both ion and gas exchange. The linings of the gut and the kidneys also become important sites of ion regulation both in freshwater and in those marine species which are osmoregulators. Only two major groups of organisms with aquatic representatives do not depend on water for oxygen uptake. Both of these groups, the insects and the amniote vertebrates (turtles, snakes and lizards, crocodilians, birds, mammals) evolved on land and breath atmospheric air (some insect larvae take up  $O_2$  directly from the water and these comments do not apply to them). Their bodies are largely impervious to water or ion exchange, yet even in these groups we commonly see adaptations similar to those in groups with more intimate contact with the water. For example, both sea birds and marine turtles have salt glands near the eyes which eliminate ions from the body, and marine mammals have highly efficient kidneys.

It can be assumed that the salt content, high or low, of a body of water has relatively little impact on the taxa which are found there, since virtually all taxa have representatives in either freshwater or marine or even hypersaline environments. The only real difference in taxa composition of communities appears when comparing terrestrial and marine habitats, which seem to be the most ecologically distinct (despite the common environmental problem of water loss faced by organisms in both these habitats). Marine habitats are essentially devoid of insects and flowering plants, two groups which coevolved on land and do not seem inclined to move into marine habitats. Competition from organisms already there is often cited as a reason, but it is more likely that there has simply not been enough time for them to evolve into marine niches. In addition, both of the terrestrial groups have life cycle adaptations that are not well-suited for open

aquatic habitats in any event. Going the other way, many marine species have not moved successfully onto land. Most cited are the crustaceans, and again, the usual reason given is competition from insects, but it is more likely that crustaceans have not moved onto land simply because they have not evolved breathing mechanisms that are effective on land; the same could be said for the echinoderms. In addition, many marine species have larval stages that could not exist on land even if the adult form could. It seems obvious to say that fish haven't made the transition to land, but this would not be accurate; fish did move onto land over 300 million years ago (MYA); we call their descendants amphibians, reptiles, birds and mammals.

Another difference between freshwater and saltwater, besides the ion concentration, is the density. Although there are probably other explanations, it is true that the largest organisms which have ever lived have been marine. Whether this is due to the greater support offered by dense seawater, or due to the fact that marine systems have larger volumes, or due to some other factor is not clear.

The depth of freshwater systems is usually much shallower than that of marine systems. As we saw earlier, depth is not a critical factor as long as the bottom of the body of water is above the LCP (light compensation point). Many freshwater bodies of water, including both rivers and lakes, have the bottom well within this range. Remember, though, that freshwater is highly susceptible to turbidity caused by soil erosion, thus the LCP might be artificially raised above the bottom. Marine systems, at least those away from the coast, are not usually affected by turbidity. The deepest freshwater lakes are about 2.7 km deep (and this occurs only in Lake Baikal, Siberia); oceans are up to 12 km deep, and the average depth of the oceans - or even the shallow part of the oceans, the *continental shelf* - is much greater than the average depth of freshwater and is almost always below the LCP.

Temperature relations in marine systems as opposed to freshwater systems are again largely dependent on the relative size of the systems. Generally, the larger marine systems show virtually no diurnal temperature shifts, and very small seasonal ones. On the other hand, small freshwater habitats may experience daily shifts in temperature of over 30 K, and pronounced seasonal temperature changes exist even in bodies of water as large as the Laurentian Great Lakes. Oceanic systems are a large part of the global weather system, which in general moves heat from the warm equator to the cooler poles. Oceanic areas exposed to currents involved in this heat transfer may be much warmer or cooler than would be expected due to their latitude alone, for instance, consider the relative warmth of the ocean near Britain due to the Gulf Stream, or the cold water off the southern California coast.

## Currents

The effect of temperature, and the allusion to currents brings us to the next topic, the flow of water. Water may flow for several reasons, but gravity is at the root of all of them. We are familiar with the simple flow of water downhill that occurs in streams. Remember, though, that water is limited in how fast it can flow. One meter per second is a very fast flow indeed in a stream; even a waterfall usually does not exceed 3 m/s. Over this speed, water separates into smaller droplets, and as the droplets decrease in size they are more easily slowed by the air. Think - rain falls from great heights, yet the speed does reach a maximum. Most freshwater currents are caused by simple gravity pulling water down a slope.

Most currents are formed more indirectly, however. Density differences, whether due to different salinities or temperatures, cause water to sink or float in relation to the water around it, and the result is a *current*. Water may also move in response to moving air (*waves*, *surface currents*, *seiches*), the gravitational pull of the Sun and Moon (*tides*), seismic activity (*tsunami*), or even the motion of the earth. With the exception of wind induced currents, most of these are more common in marine systems and we will examine them in turn.

Air is sent in motion by density differences due to differing temperatures. For instance, air heated over a land mass during the day will rise and be replaced by cooler air flowing from a body of relatively cool water nearby (an *onshore breeze*, the opposite, an *offshore breeze*, occurs when the water is warmer than the land). As the air passes over the water, it causes the water to move along with it. This effect is strongest at the surface and decreases with depth. Since the water near the surface is moving faster, it piles up in waves that are constantly breaking down as gravity pulls on the water. A stronger wind will be able to pile up more water, thus creating larger waves. Very strong wind can whip the water at the edge of the waves into a frenzy of foam, these waves are known as *whitecaps*. Waves being actively formed by wind typically have short wavelengths and are known as *chop*; long, low, smooth waves from storms long past are known as *swells*. The distance of water over which the wind passes is known as *fetch*; the greater the fetch, the greater effect the wind will have. A structure (ship, shore, breakwater, etc.) typically has a *weather* side exposed to the wind and waves; the side away from the winds is the *lee* side.

It is generally known but poorly understood that waves cause as much vertical as lateral displacement of the water particles themselves, and that there is little net movement of the water particles. The motion of the average water particle as a wave passes a fixed point is circular; it rises, moves forward, falls, moves backward, and rises again. The circular movement of water near the surface sets up similar, smaller circular patterns in the water below to a depth equal to about 1/2 of the wavelength of the wave (Fig. 1). Actually, what is moving are the high and low points in the water, not the water itself. Still, if all the high points are moving in the same direction, this will cause a net flow of water (a surface current).

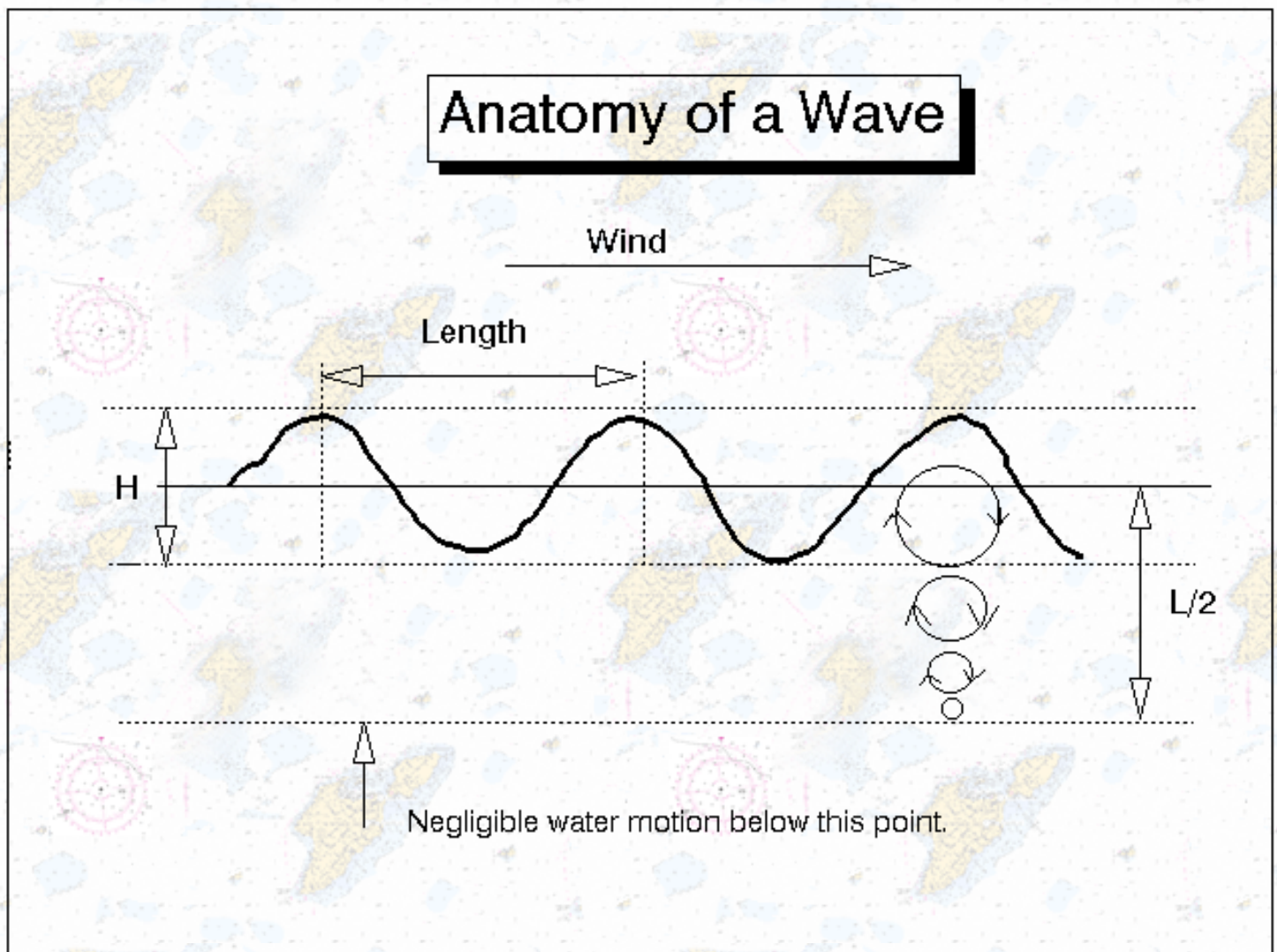


Figure 1. Water motion in a wave. Wave height is indicated by H; wavelength is the distance between the tops of adjacent *crests* (or the bottoms of adjacent *troughs*). The circles indicate the relative motions of water particles at different depths; wave-induced water motion decreases with depth, and is negligible below a depth equal to 1/2 the wavelength. There is some small net movement of the water particles in the direction of the wind.

The waves may bounce off solid objects and be reflected back into the open water; under these conditions the water surface can be a very confused place with waves moving in all directions simultaneously. On other shores, the energy of the wave is dissipated as it *breaks* on the shoreline. Breaking occurs as the water particles reach shallow water where they cannot complete the bottom part of their circle. They hit the bottom and slow down. As they slow down, more water comes in from behind and the wave grows taller, with the top moving faster than the bottom. This obviously cannot continue for long, and eventually the wave topples over, or breaks. Waves with long wavelengths break in deeper waters, and an experienced eye can judge wavelength and determine depth by where the waves are breaking. Particles proportional in size to the size of the wave may be picked up from the bottom and moved shoreward by the waves, a process known as *onshore transport*. Water flowing back from breaking waves is known as *undertow*, and constitutes a current in its own right. If the waves approach the shore at a slight angle, a *longshore current* will develop along the beach. The longshore current moves parallel to the beach in the opposite direction to that from which the waves approach. The longshore current can be an important factor in shaping the shoreline by distributing the material brought in by onshore transport. At various points, the longshore current will abruptly turn seaward and form a *rip current*, a sudden return flow to the ocean (lake). Such rip currents may carry unwary swimmers out to sea; it is nearly impossible to swim directly against them. The best strategy is to remember that they are often quite narrow and to swim perpendicular to the rip current until clear, then swim back to shore.

In a lake, water can pile up at one end of the lake due to a consistent wind from one direction. When the wind stops, the piled up water will flow back to the other end. This is known as a *seiche*, and can easily be replicated in a bathtub by using your body to pile up the water at one end. After the water sloshes back, it usually overshoots by some margin, and

ends up piling up at the other end, the sloshing back, etc., for some time (Fig. 2). Of course, each successive slosh is less than the previous one, and in a lake, the only really noticeable differences occur during the wind (the set-up) and during the first seiche. Seiches may become quite complicated in lakes stratified by temperature or salinity differences as the lower levels will slosh at a frequency different than the upper ones. This sloshing of the lower levels is known as an *internal seiche*.

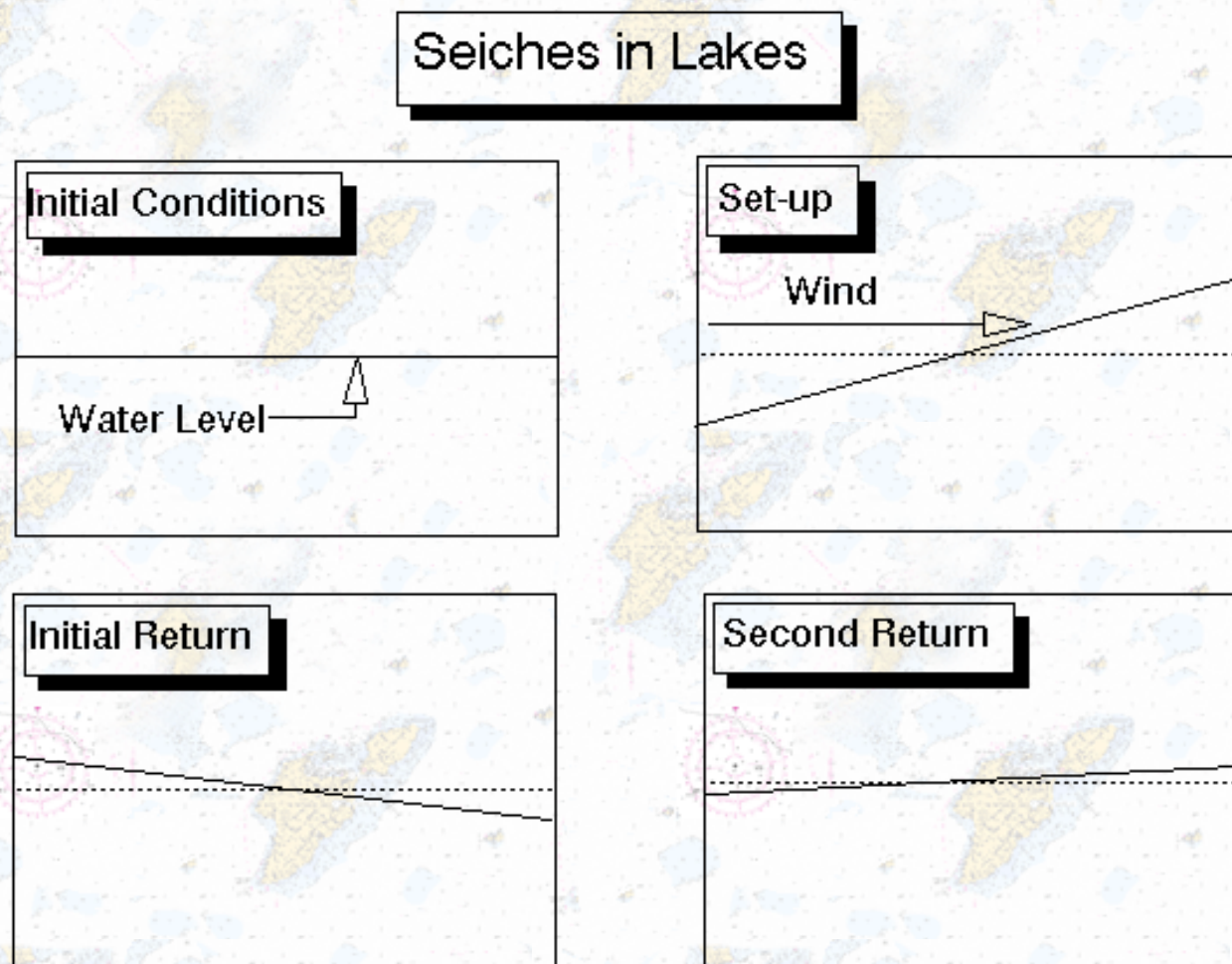


Figure 2. Action of a seiche. In the upper left drawing, the lake is at its normal level. In the upper right drawing, a consistent wind piles water up at one end of the lake. In the lower left, the wind stops and water flows back in response to gravity. Momentum of the flowing water causes the return flow to be greater than the original volume of water in that part of the basin, resulting in higher than normal levels. Gravity acts on this elevated water and causes it to flow back to the far side of the lake in the lower right picture. The oscillations decrease in magnitude each time. Vertical scale greatly exaggerated.

Tides occur when the gravity of the Sun and/or Moon acts to slightly offset the gravitational pull of the Earth, allowing the water to rise slightly. It is easiest to think of this as if the sun and moon remained stationary and the Earth revolved under them. Wherever the Sun or Moon is directly overhead, there is a slight bulge in the ocean. A similar bulge is also seen on the opposite side of the planet due to centrifugal force. As the position of the Sun and Moon changes in relation to the surface of the Earth, the bulge seems to move. When the bulge approaches a shore, this results in an apparent *high tide*; the areas exactly halfway between the two bulges are experiencing *low tides* at the same moment. Lunar tides are more apparent than the solar tides and thus it is the motion of the Moon, which circles the Earth every 25 hours, that determines the number of high tides (2) which will occur each day.

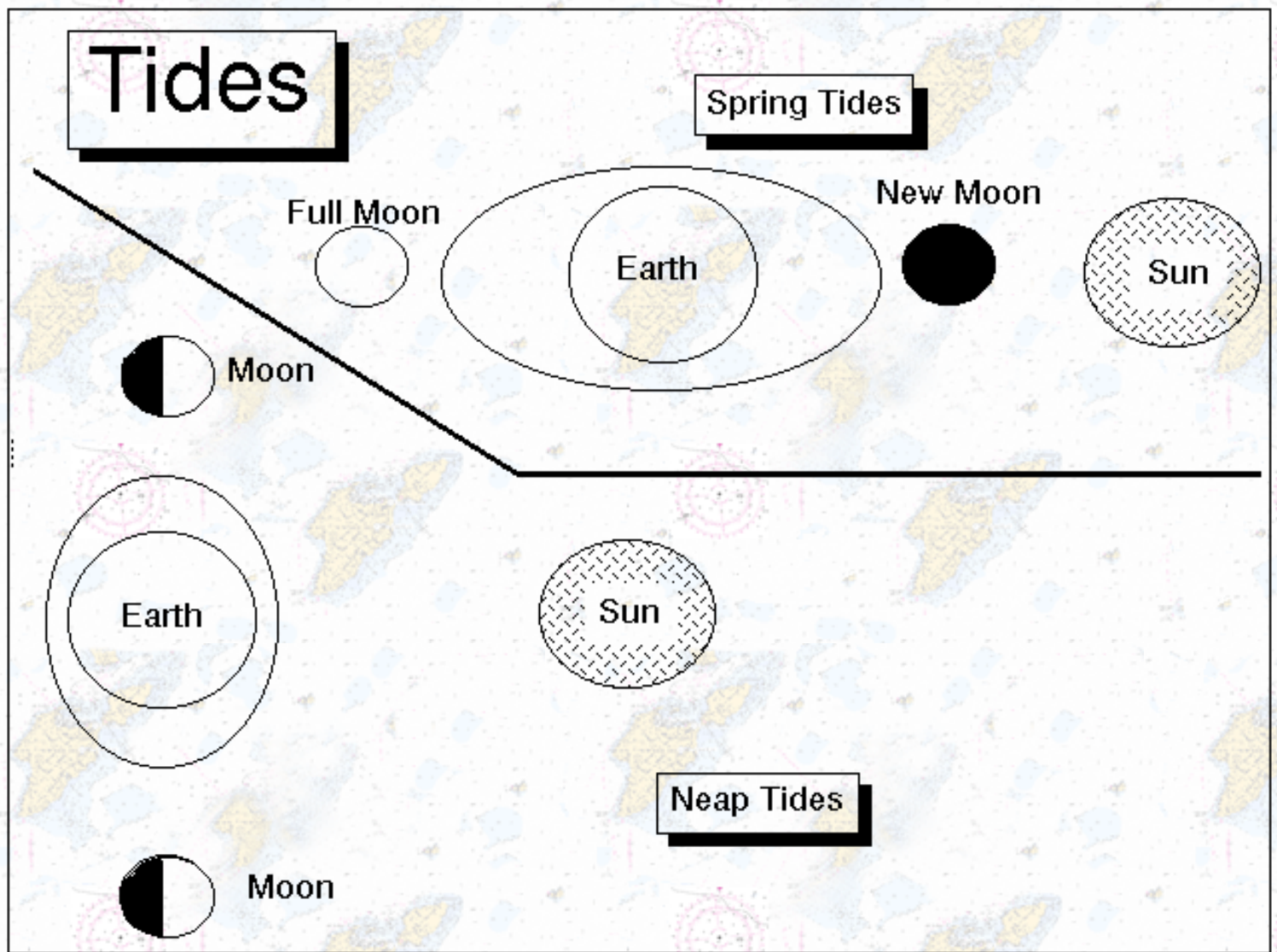


Figure 3. Tides. The ellipse around the Earth represents a greatly exaggerated profile of the tide. Neap tides occur when the gravitational pull of the Sun and the Moon reinforce each other (every two weeks at full or new moons); spring tides occur when the Moon is at right angles to the Sun (every two weeks at half moons). Obviously not to any kind of scale.

When the Sun and Moon are in alignment (on the same plane) they will reinforce each other's gravitational pull. Thus, whenever there is a full or new moon (every two weeks) the tides will be particularly high and low and are referred to as *spring tides* (Fig. 3). Whenever the Moon is a half crescent (half moon, every two weeks) the Sun and Moon are at right angle to each other and cancel each other out to some extent. This results in minimal tidal ranges or *neap tides* (Fig. 3).

The effects of shoreline shape, ocean basin shape, winds, tidal currents, etc., combine to produce variations from the ideal *semidiurnal* (twice-daily) pattern pictured above. Such a pattern does exist on the eastern coast of North America, and in several other places in the world, but other areas may only experience *diurnal* (once daily tides) or even no tide at all. The size of the tide is also affected by such patterns; generally open shorelines show less tidal range than funnel-like estuaries such as the Bay of Fundy where the daily tidal range is over 10 m. When such a high tide sweeps up an estuary it can meet the water flowing down to the sea and form a wall of water known as a *tidal bore*; the Amazon River has a particularly dramatic tidal bore on some of its distributaries.

*Tsunami* are often called tidal waves because they mimic tides. Tsunami (a Japanese word, the Japanese, living on islands in an area rich with seismic activity have had long experience here) are generated whenever a shift in the Earth's crust displaces water. For instance, when California finally slides into the sea, water will have to move out of the way (this can be simulated by sitting down abruptly in the bathtub, or by doing a cannonball, preferably *not* in the bathtub, as your mother has no doubt told you). This water travels away at very high speeds, and, at sea, is hardly noticeable. The problem occurs in coastal areas where the tsunami reaches shallow water. The shallow bottom drags on the wave, and the traditional process of wave breaking begins - but with a much larger wave to deal with. As with tides, the effect is pronounced in enclosed areas such as bays. Since people concentrate in such areas, which normally offer protection from wind-formed waves, there is considerable potential for loss of life when a tsunami reaches such a point. Much of the loss of life surrounding major volcanic events in the South Pacific was due to tsunami rather than the volcano itself, since most island people are smarter than to live near an active volcano (sacrificing virgins all the time does not lend itself to

population enhancement). Tsunami can also form when a *rift* opens in the ocean floor as two plates move apart (try separating your hands or legs underwater in the bathtub). On a much smaller scale, the sudden entry into the water of a large chunk of ice from a glacier may cause a small tsunami; occasionally these are of sufficient size to swamp boats or do other localized damage.

The rotation of the Earth itself will affect the flow of water (or air) once gravity or other forces have put it into motion. Imagine a current heading north in the Northern Hemisphere. The Earth is rotating to the east, and the water picks up that momentum. The Earth rotates fastest at the equator, and slowest at the poles. Therefore, as our water travels north, it moves to a part of the planet that is not moving eastward as fast as the water itself is. Therefore, the water current ends up moving eastward as well, resulting in a current that curves to the right. This effect is called the *Coriolis effect*; it is most pronounced at the poles and weakest at the equator. It has effects on virtually all moving water or air on the planet. Its effects are the opposite in the Southern Hemisphere, where currents tend to curve left. For somewhat obscure reasons, winds around low pressure zones act differently. Wind around a low pressure zone in the Northern Hemisphere rotate counterclockwise (to the left) because of this force; storms in the Southern Hemisphere rotate clockwise for the same reason. Remember that a storm is simply air moving towards a region of low pressure or away from a region of high pressure; such currents would normally be in a straight line were it not for the Coriolis effect.

The directions of flow do not hold true for bathroom fixtures; for instance, if you take your sink to Australia the flow will not necessarily reverse itself. My sink drains clockwise, but my toilet flushes counterclockwise; obviously basin morphology and design (in my toilet's case the little streams of water are set up to induce counterclockwise flow) can override the Coriolis effect, at least in small containers. Another factor in determining which way the water will flow in a small system is *chaos theory*. Basically, chaos theory examines the many systems which appear to be random, but in fact are deterministic. Usually, in chaotic systems, oscillations may occur which make the system unpredictable, but, if the physics underlying the phenomenon can be expressed in mathematical equations, it is usually possible to show that for a given set of initial conditions, the outcome (direction of fluid flow, population size, heart rate) will be the same, however messy. The problem with predicting what a chaotic system will do involves the impossibility of knowing (with enough detail) exactly what the initial conditions are. For instance, it has been said that a butterfly flapping its wings in Mexico could have an effect on a hurricane in the Caribbean. Chaos theory is new; it is having a profound effect on the way we see many biological phenomena; and it ultimately explains why weather forecasting will never be an exact science no matter how powerful our computers become.

In the open ocean, the Coriolis effect leads to another phenomenon, the *Ekman spiral*. As the wind, for instance, blowing north, starts to move the water at the surface in that direction, the Coriolis effect deflects the water at a  $45^\circ$  angle (to the right or left, depending on hemisphere). As this water moves out, it also pulls along the water below it, but, again, the Coriolis effect pulls *this* water  $45^\circ$  ( $90^\circ$  to the original wind), and so on. Summed over depth, the net flow of the water is about  $90^\circ$  to that of the wind. Thus, in the Northern Hemisphere, a wind coming from the east (an easterly) will result in a current to the north. In the oceans, these currents interact to form huge circular currents or *gyres* (Fig 4).

*Disclaimer:* Be very careful when doing your homework not to spill water out of the tub. If you get in trouble with your mom, RA, landlord, etc. it is your own fault and I didn't make you do it. You're grown-up now. Try to keep the splashing to a minimum (bubble bath helps hold down the noise). Also, note that the majority of these experiments will not work with two people in a standard American bathtub, so despite my usual admonitions to work together, this isn't a good time to do so. I hereby release myself from all claims of water damage to carpets, floors, rubber ducks and other household artifacts.

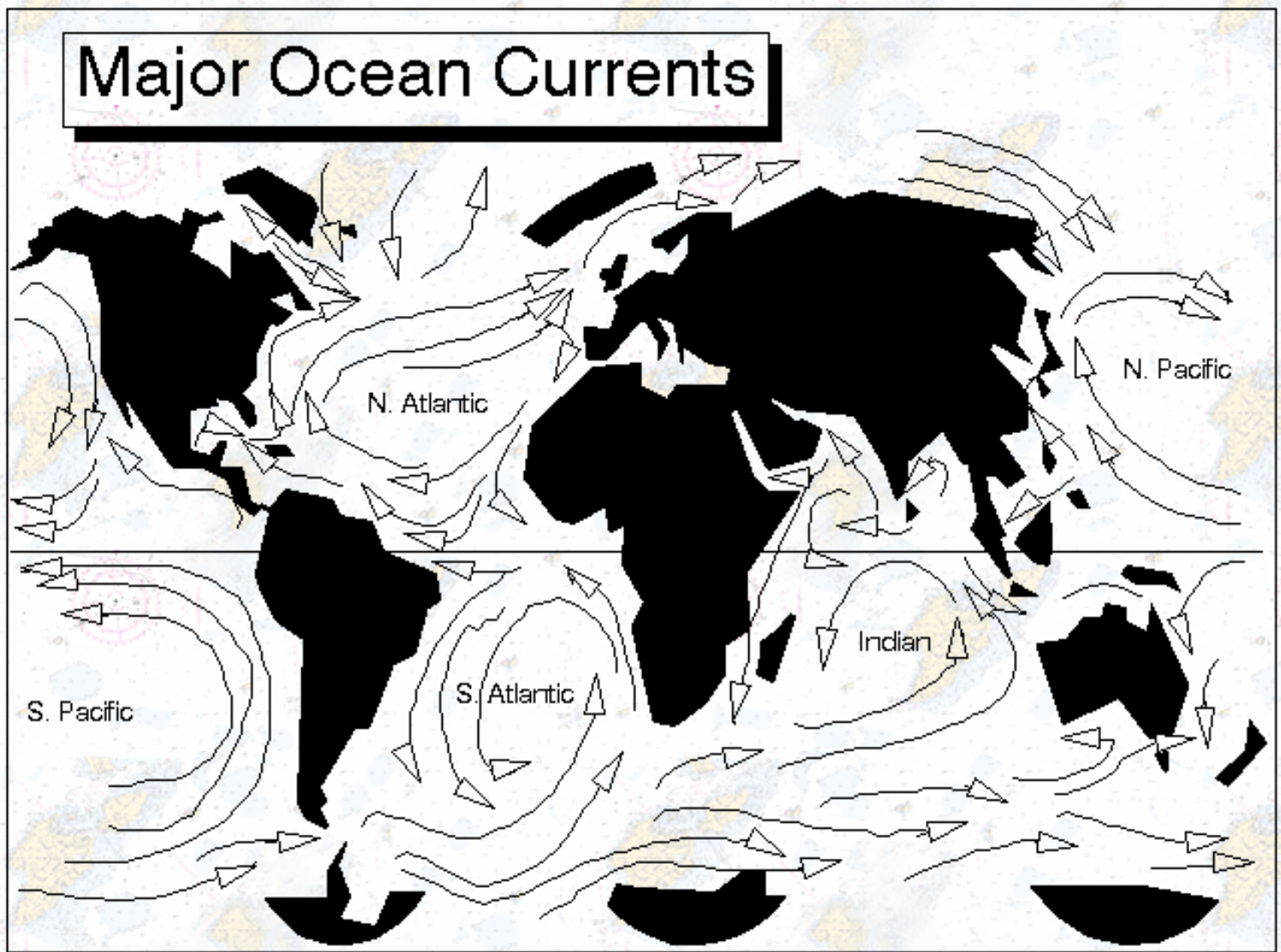


Figure 4. Major ocean currents. Note in particular the gyres formed in each of the main oceans (2 each in the Atlantic and Pacific). The gyres do not usually cross the equator, but do set up strong equatorial currents. Note that the Gulf Stream (not labeled) carries warm water from the equator northward and thus warms Europe; similar warm currents include the Japan Current in the northern Pacific, the Agulhas Current warming southern Africa's eastern coast, and the Brazil current warming the eastern coast of Brazil. In the southern hemisphere there is relatively complete circumpolar flow; in the northern hemisphere land masses prevent such flow. Note also the secondary gyre formed north of the Gulf Stream.

## Lentic Systems

Aside from the comparison between marine and freshwater systems, we should also make a distinction between *lotic*, or running waters, and *lentic*, or still waters. These distinctions, of course, make sense only in freshwater; the entire ocean is lentic, although small areas swept by strong currents might somewhat resemble a lotic system. We will examine lentic systems first.

Lentic systems form when water is trapped at a level above sea level (or below sea level without an outflow). We call large lentic systems lakes, smaller ones ponds. Ponds and lakes form when something blocks a stream, such as a mudflow, avalanche (*cirque* lakes), beaver, or human. Even more lakes form in natural depressions such as old volcanic craters (*caldera* lakes), earthquake rifts (*graben* or *rift* lakes) or low-lying areas. Glaciers may scoop out depressions (the Laurentian Great Lakes), or leave behind large blocks of ice in the soil (*till*) they deposit as they retreat. The block of ice creates a void (hole) in the till, and as the ice melts it fills the hole (*kettlehole* lake).

Many characteristics of a lake are consequences of its basin and its *catchment*. The basin, as explained above, determines the lake's size, shape and depth. For instance, glacial lakes tend to be very deep, while beaver ponds are shallow. The catchment is the area of ground surrounding the lake that contributes water to it. All of the streams and/or rivers upstream of the lake (*feeders*), and the water they drain from the surrounding land contribute to the catchment. Subsurface water (*groundwater*) may also contribute water to lakes. The nature of the soil and rock in the catchment will have a great impact on the water chemistry of the lake. For instance, glacial lakes are often surrounded by swampy land (*bogs*), and these bogs produce large amounts of moss, which sinks under the water and begins to decay. Because it

decays slowly, under anaerobic conditions, acid conditions prevail, and the water in a glacial lake is often stained with dark brown humic acid. Lakes in areas with lots of limestone are often very alkaline. Land use within the catchment will also affect the water in the lake; farming the land will contribute soil (eventually filling in the lake), fertilizers and pesticides; cities will mean rapid runoff after storms because water flows off pavement rather than sinking in, and oils, salt, etc. from city streets will enter the lake.

Another important concept in lentic systems is *residence time*. Residence time is simply the average amount of time water spends in the lake. It can range from minutes to years; for instance, in Lake Erie it is about 2.5 years. Another way of looking at residence time is to empty the lake and see how long it takes to fill. This obviously is not practical for most lakes. The residence time affects many things, including water chemistry. If, for instance, a dangerous chemical is accidentally dumped into two lakes, the lake with the shorter residence time will be able to flush out the toxin more quickly. In certain saline lakes, where there is no outflow, residence time may be short for the water (due to high temperatures and rapid evaporation), but no flushing will occur.

Because there is no single, directional flow in a lentic system, *stratification* may occur. Stratification is the horizontal partitioning of a lake into *strata*, layers of water that do not mix. The basis for stratification is usually density differences induced by temperature, however, other factors that change density, such as salinity, also may be responsible. In a typical lake in a temperate climate, stratification normally manifests itself in the formation of two layers, a warm upper *epilimnion*, and a cool, lower *hypolimnion*.

It is perhaps easiest to see how stratification works by examining a typical temperate lake throughout the year. In the summer, the sun warms the upper levels. Since warm water is less dense, it tends to float, and the warm water concentrates at the surface. Between the warm upper water layer, and the cool, dense water below, there is a zone of rapid temperature change, the *thermocline* (Fig. 5). The thermocline is not necessarily a sharp plane, often the zone of temperature drop may extend for several meters. The depth and thickness of the thermocline are affected by the lake basin, wind, insolation, and other factors. Obviously, shallow lakes may warm all the way to the bottom and not exhibit a thermocline. In other shallow lakes, the bottom layer may be fed by springs; in such cases the thermocline may be quite abrupt; you may have experienced such thermoclines when swimming in a pond.

The division of the lake into these two zones has a profound effect. The epilimnion is mostly above the LCP for many organisms, and these organisms quickly use up all the nutrients as they photosynthesize. The wind may mix the upper layer, insuring ample  $O_2$  throughout, but the hypolimnion will not be mixed because the density difference is too great for the wind to overcome. The hypolimnion, below the LCP for most organisms, will become anoxic. As organisms in the epilimnion die, they will fall to the hypolimnion, carrying essential nutrients with them, and, in the hypolimnion, even more  $O_2$  will be used in their decay, exacerbating the  $O_2$  deficit there. Anaerobic respiration will become the rule, and bacteria which can survive under these conditions may add things like methane and  $H_2S$  to the water, making it acidic and smelly.

# Thermocline in a Stratified Lake

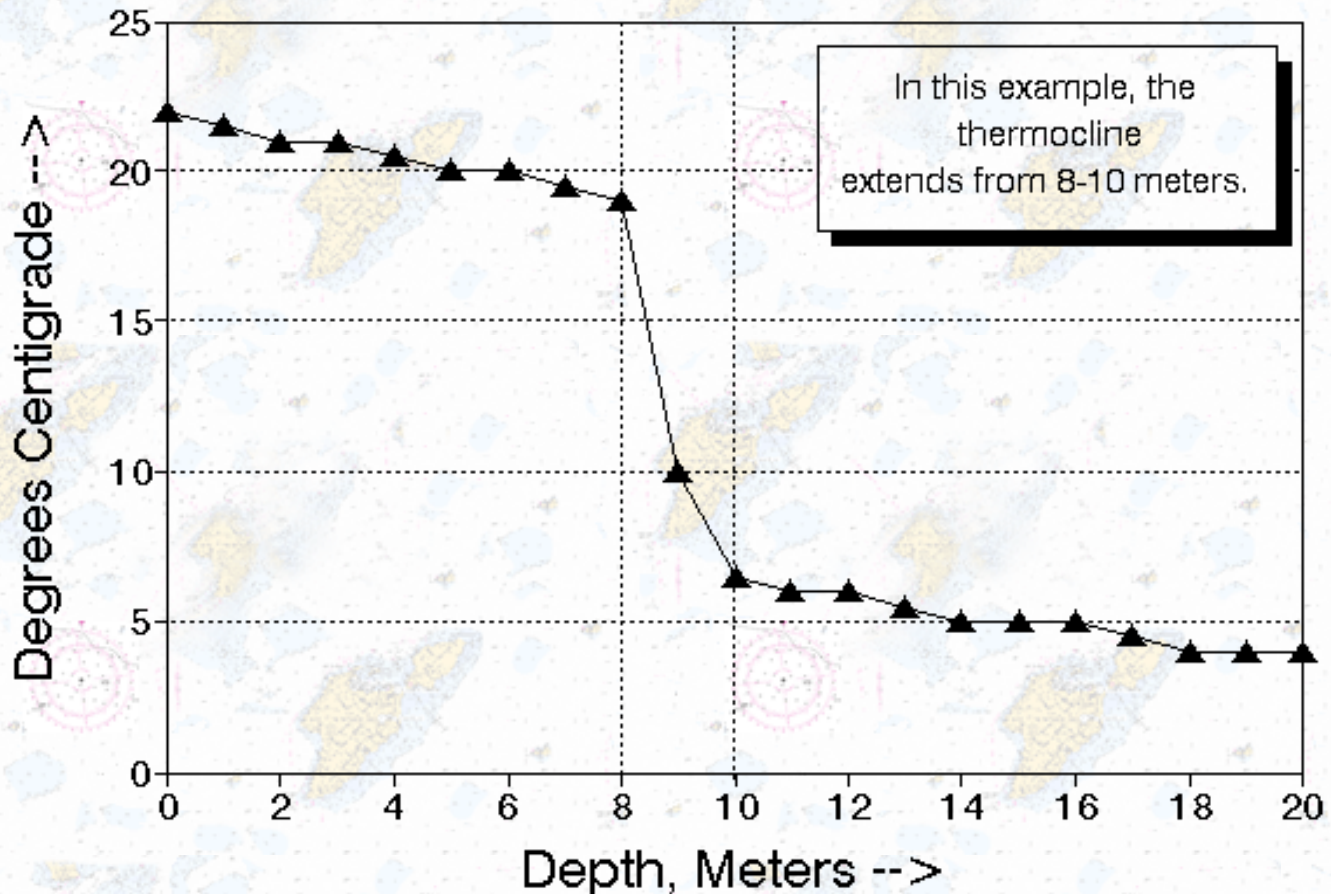


Figure 5. Graph showing a temperature profile of a stratified lake. In this example, warm surface waters (epilimnion) persist to a depth of about 8 meters, where they meet the cold, dense water of the hypolimnion. The zone where the temperature changes rapidly, from 8 to 10 meters, is the thermocline.

Some organisms take advantage of the differences between the hypolimnion and epilimnion. Because of the lack of  $O_2$ , most fish avoid the hypolimnion, and thus it becomes a refuge from fish predation for the organisms which can live there. *Chironomus* larvae (which will grow up to be midges, which resemble mosquitoes but don't bite) have hemoglobin very similar to ours (2 subunits rather than 4); they can absorb  $O_2$  from the water even at low  $O_2$  levels. The *Chironomus* larvae (a.k.a. bloodworms) feed on bacteria, which, as mentioned above thrive on the rain of detritus (decaying organic material) from above. *Chaoborus* larvae (the adults of which look a lot like midges and mosquitoes, and also don't bite) are predators themselves; these bizarre-looking, transparent (they are called phantom midges), larvae hide at the bottom during the day, then rise up to the epilimnion at night to feed on plankton, presumably when capture by fish (which often rely on sight to capture prey) will be less likely. *Chaoborus* larvae make their vertical migration with the aid of small air sacs in their bodies; they can add or subtract air from these sacs to alter their density. Such diurnal vertical migrations are even more common in marine systems.

As summer ends, the amount of heat gained by insolation during the day will be less than the amount lost by radiation of heat at night. The surface waters will radiate heat to the atmosphere at night, cool, become more dense, and sink. Eventually, the whole water column will be at the same cool temperature. At this point, any wind pushing on the surface water can cause the water to be set in motion, and the water from the bottom is free to mix with that on the surface. This mixing is an important time for life in the lake. It allows the nutrients which have accumulated on the bottom to come to the surface, and it also allows  $O_2$  to reach the bottom of the lake.

Stratification of a different type will occur when the lake freezes in the winter. Here the surface water (ice) is much less dense than the other water and thus floats on top. Ice cuts down on  $O_2$  exchange, but this is not as critical in the winter when the cold temperature has slowed down the metabolic rates (and thus  $O_2$  demands) of most of the organisms in the water. Still, long ice covers may cause fish kills. Snow cover on the ice may drastically reduce light levels also, but, most

importantly, the ice and snow cover reduce heat loss from the lake and thus reduce the likelihood of the lake freezing completely. Underwater springs and flowing water coming into the lake also contribute some crucial warmth at this time.

In the spring, the ice melts and the water is again at a constant temperature throughout the water column; in large lakes this temperature is 4° C at both the fall and spring *turnover* (mixing). Again, this mixing allows nutrients from the bottom to enter surface waters, and allows O<sub>2</sub> to reach the bottom. Often a *bloom* (massive growth) of algae will occur at this point. The city of Akron obtains its drinking water from a lake; you can estimate when spring turnover has occurred by the taste and smell of the water, which is affected by blooms of the alga *Dinobryon*. Soon, increasing insolation begins the process of stratification by warming the surface waters (although strong storms will cause mixing for some time). If you can measure the levels of plant nutrients in the epilimnion, or the level of O<sub>2</sub> in the hypolimnion, you have a pretty good idea of the limits on biological processes that will constrain those two habitats for the summer (but remember that additional plant nutrients can enter the surface waters). The process of cultural eutrophication contributes to both algal blooms in the epilimnion and oxygen deficits in the hypolimnion; such effects are much less common in oligotrophic lakes.

A lake that exhibits two periods of mixing separated by two periods of stratification is known as a *dimictic* lake. There are also *monomictic* lakes, usually in warmer climates where the lake doesn't freeze (or in some large lakes in cooler areas); *polymictic* lakes which mix constantly; and *oligomictic* lakes which are often found near the equator, remain stratified year-round, and thus rarely mix. Mixing of a lake may be complete (*holomixis*) or incomplete (*meromixis*).

### Benthic Sediments in Lakes (and streams)

Benthic sediments are often very much like the parent rock of the surrounding watershed. Often, waves or currents will sort the bottom sediments into areas of uniform sizes. The chief means of characterizing sediments is based on size:

Name	Diameter (mm)	Diameter (phi units)
Boulder	>256	< -8
Large cobble	256 - 128	-8 to -7
Small cobble	128 - 64	-7 to -6
Very large pebble	64 - 32	-6 to -5
Large pebble	32 - 16	-5 to -4
Medium pebble	16 - 8	-4 to -3
Small pebble	8 - 4	-3 to -2
Granule	4 - 2	-2 to -1
Very coarse sand	2 - 1	-1 to 0
Coarse sand	1 - 0.5	0 to 1
Medium sand	0.5 - 0.25	1 to 2
Fine sand	0.25 - 0.125	2 to 3
Very fine sand	0.125 - 0.0625	3 to 4
Coarse silt	0.0625 - 0.03125	4 to 5
Medium silt	0.03125 - 0.015625	5 to 6
Fine silt	0.015625 - 0.0078125	6 to 7
Very fine silt	0.0078125 - 0.0039063	7 to 8
Coarse clay	0.0039063 - 0.0019531	8 to 9
Medium clay	0.0019531 - 0.0009766	9 to 10
Fine clay	0.0009766 - 0.0004883	10 to 11

Note the small size of the boulder (down to about 1 foot) in terms of what you normally consider to be a boulder! Generally, in a lake, the coarse sediments settle out near the inflows at the edges of the lake, and finer sediments will predominate in the profundal benthos.

In addition to the inorganic material, considerable organic material will settle to the bottom of lakes. This material may be modified by organisms living near the bottom and take on several forms, including *gyttja* or *copropel*. This material is largely formed by decaying plankton settling to the bottom, being eaten by bottom dwelling organisms such as *Chironomus*, and excreted as feces (*Kopros* Gr.: dung). It is gray or dark brown in color, and may appear gelatinous or as small pellets. The layer of copropel is thicker in eutrophic lakes. *Sapropel* forms when bottom sediments do not obtain sufficient O<sub>2</sub>; it is black in color and smells like rotten eggs due to the presences of H<sub>2</sub>S and methane. Formation of

sapropel is another indication of eutrophic conditions.

Overall, several zones can be delineated in a lake (Fig. 6). The benthic habitats include the *littoral zone*, where enough light reaches the bottom to support plant growth, and the *profundal zone*, which is below the LCP and often below the thermocline as well. The habitats in the water column include the littoral zone, where plants are present, the open water area above the LCP known as the *limnetic zone*, and the area below the LCP which is also called the profundal zone. The epilimnion and hypolimnion are also present in stratified lakes and may or may not correspond to the neritic and profundal zones.

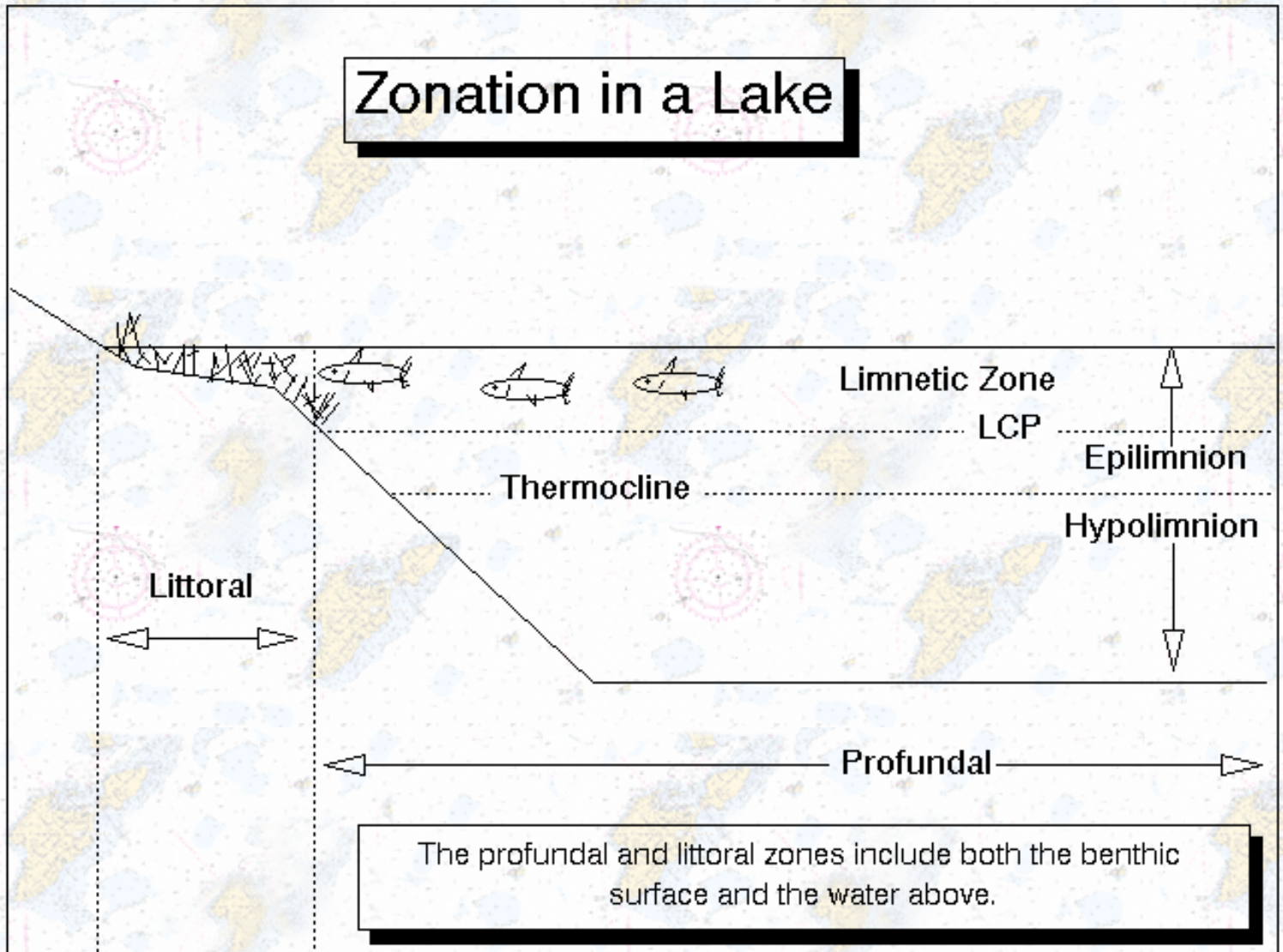


Figure 6. Habitats in a lake. The littoral zone rings the lake and includes that portion of the water column where plants emerge from the water, or that portion of the bottom where rooted plants are found. The limnetic zone is the open water above the LCP; the profundal zone is the water below the LCP and the benthic areas below. The thermocline is an area of rapid water temperature change with increasing depth; it exists only in stratified lakes and divides the water column into an upper epilimnion and lower hypolimnion. The epilimnion and hypolimnion correlate with the limnetic and profundal zones only when the thermocline is located at the LCP.

### Lotic Systems

Again, the main distinction between a lotic system and a lentic one is the presence in lotic systems of a unidirectional gravity induced current. Another way of looking at a lotic system is to think of it as a series of overlapping lentic systems with very short residence times. In many ways, lotic systems resemble lentic ones, and we will focus here on the differences.

You are no doubt familiar with many of the names given to lotic systems. Generally, in order of increasing size they are: seeps, springs, streams, rivers. There are also creeks, cricks, rivulets, and so on. Be particularly cautious of the habit in the western U.S. to name every drainage ditch a river in honor of the 2 hours every ten years they actually achieve such flows. This practice no doubt grows out of nostalgia for water, and to compensate for the eastern habit of naming large hills mountains.

The current dominates lotic systems. As mentioned earlier, current speeds can get up to about 3 m/s, but most rivers have currents less than 1 m/s; many "fast" streams are actually flowing about 0.3 m/s, and large rivers have deceptively fast currents. Remember also that the average current speed does not take into account the areas of fast flow (near the surface in deep water) and slow flow (along the bottom and edges, behind obstructions) that may exist. Many small streams are actually series of lotic fast water and small pools that are essentially lentic.

Current meters, both mechanical and the time honored timing of an apple (density near that of water, floats but is not affected by wind, bright red, easily visible, cheap, biodegradable, nutritious) over a measured distance, only measure average current speed, and about the only thing you can say about average speed is that it is the speed that most organisms are *least* likely to encounter as they crouch behind and under rocks, logs, etc. In addition, there is the *boundary layer* (Fig. 7). As Stephen Vogel puts it, the boundary layer is perceived by most as a fuzzy notion that it's a discrete region rather than as a discrete notion that it's a fuzzy region. The boundary layer is defined arbitrarily by humans; it refers to the fact that a fluid flowing over a surface tends to "stick" to the surface, so that at the surface the fluid speed is essentially zero, and it increases rapidly. Engineers usually define the boundary layer as the area in which current speed is up to 99% of the undisturbed current speed; biologists typically use 90% as the cutoff point (I *told* you it was arbitrary).

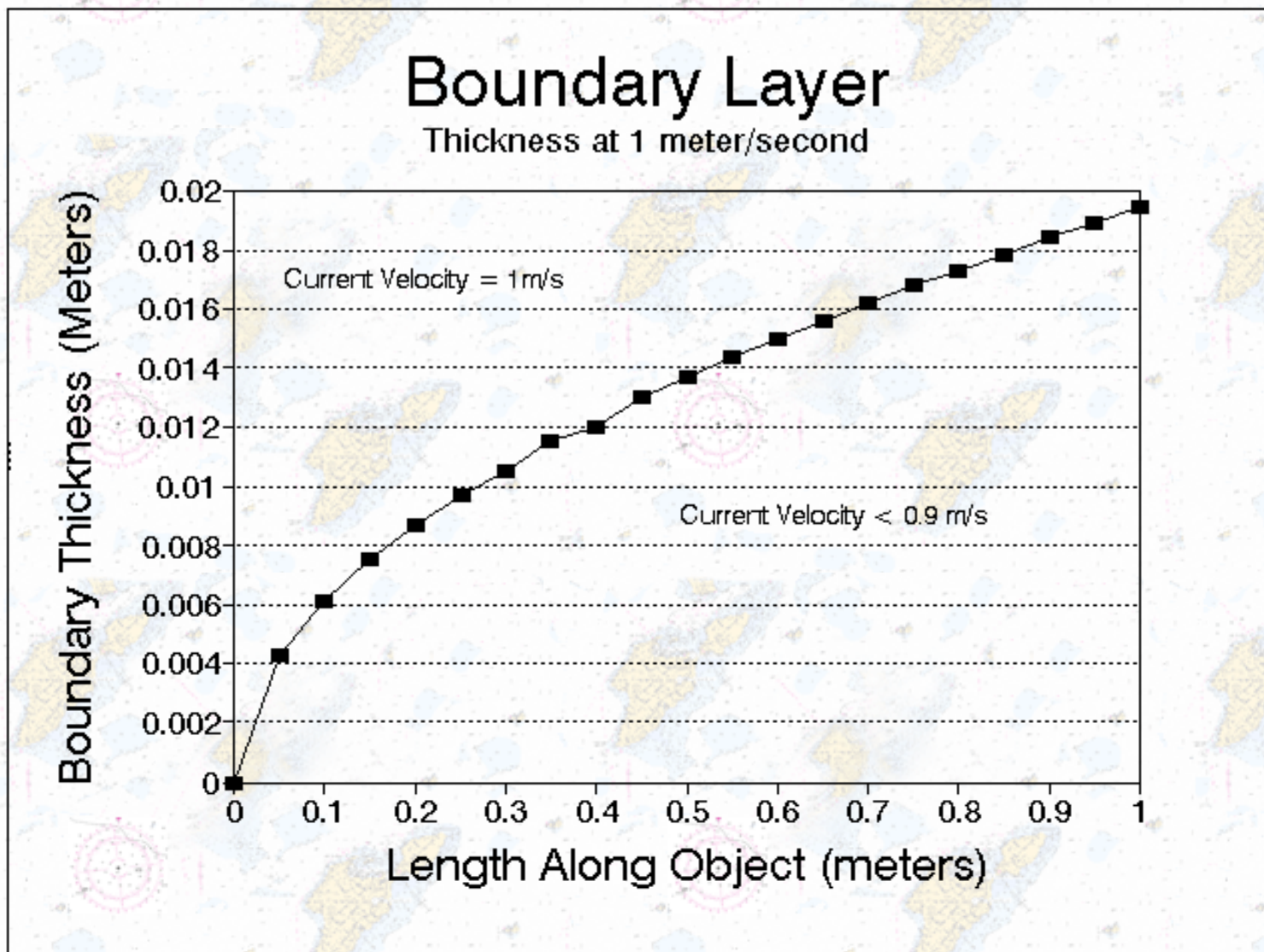


Figure 7. Graph showing height above the substrate where the current speed is 90% of the mean current velocity (1 m/s). Note that the further back one goes from the front surface of an object placed in the current (moving to the right along the horizontal axis), the thicker the layer becomes. Note also that the layer in this example is always quite thin (up to 2 cm here), and that even within the boundary layer the water is anything but stagnant. Current speed will decrease to zero at the water-substrate interface. A higher current speed would result in a boundary layer curve displaced down and to the right.

The boundary layer gets thicker as current speed gets smaller, and gets narrower as you approach the front edge of a surface exposed to flow. The boundary layer is thus wider at the back of a rock in the stream than it is near the front edge, and, if current speed increases (say, after a rain), the boundary layers in both locations will grow narrower. If you doubt the existence of the boundary layer, look at the blades of a fan, and figure out why the dust there doesn't blow off when the fan is turning. The reason, of course, is that the dust is well within the boundary layer and thus not exposed to the air currents. In streams, only microorganisms are small enough to escape the effects of the current by living in the

boundary layer; most multicellular organisms are simply too big even if they are highly flattened (see McShaffrey and McCafferty, 1987 for more on this).

Because of the costs involved in trying to maintain position in a current, most organisms in lotic systems are benthic, and hold onto the bottom in one of the ways mentioned above. In general, benthic organisms in streams have more elaborate holding mechanisms than those in lakes; these holding mechanisms include such things as silk which is used by insects in very fast currents. Organisms in streams also tend to be more streamlined (because of the higher  $Re$  - remember) or flattened, however recent studies (McShaffrey and McCafferty 1987, Craig 1990) show other reasons for being streamlined such as the ability to inhabit crevices or to accelerate quickly. Remember too that the direction of the current as it swirls around rocks and other obstructions may not be as unidirectional as the net flow of the stream is. Furthermore, the swirling motion is chaotic, hence unpredictable, for most organisms - they must be prepared for the current to switch suddenly.

A strong current means that plant nutrients and gasses such as  $O_2$  will usually be mixed throughout the water column, allowing good gas, nutrient, and waste exchange for those organisms which can keep a grip. Plankton do not do well in lotic systems, however, since they may be swept into areas unfavorable for growth. Attached algae may also suffer since moving water can carry soil particles in suspension, blocking out light and raising the LCP above the bottom. The ability of the water to carry and move particles varies with its speed, and the deposition of those particles, which occurs as the water slows down, affects the distribution of different size particles on the bottom of the stream. Because of the chaotic nature of the currents, soil particles on the bottoms of streams tend to be more patchy and mixed than those in lakes, and will often shift position.

It is possible to divide the stream into different habitats; these habitats differ mainly in current speed and the resulting nature of the substrate (Fig. 8). Areas where the current is capable of lifting particles from the bottom are known as *erosional* habitats; areas where particles are coming out of suspension are known as *depositional* habitats. The distinction is a bit fuzzy, since it really depends on what size of particle you are talking about; usually we refer to the erosional or depositional areas in terms of silt or fine sand. Among erosional habitats, we can distinguish *riffles*, where at least some rocks break the surface and there is active mixing of air and water, and *runs*, where the water moves faster but is deeper than the rocks, and which has cobble or larger particles for substrate. Depositional areas are typically called *pools*, with bottoms of sand or silt.

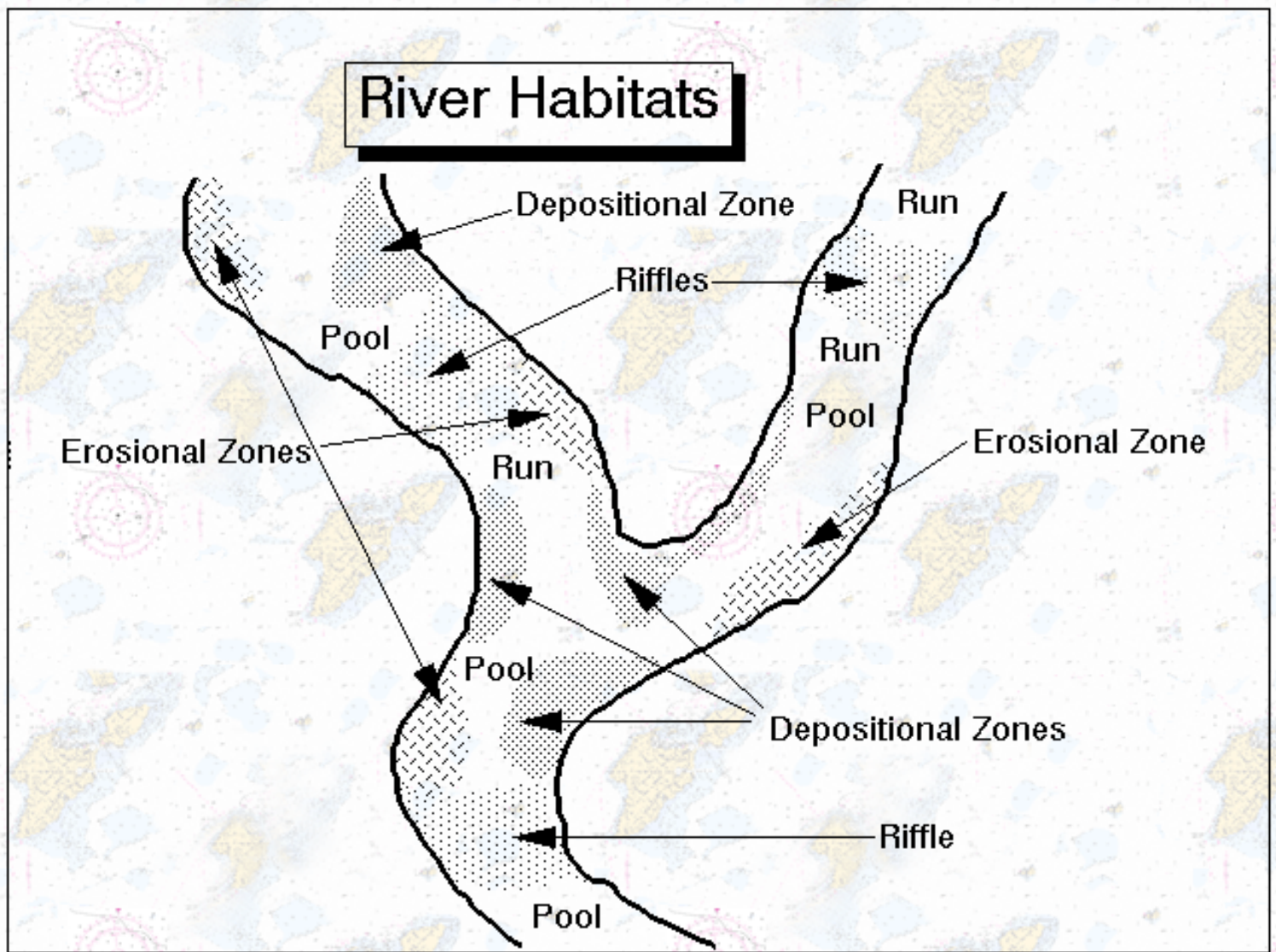
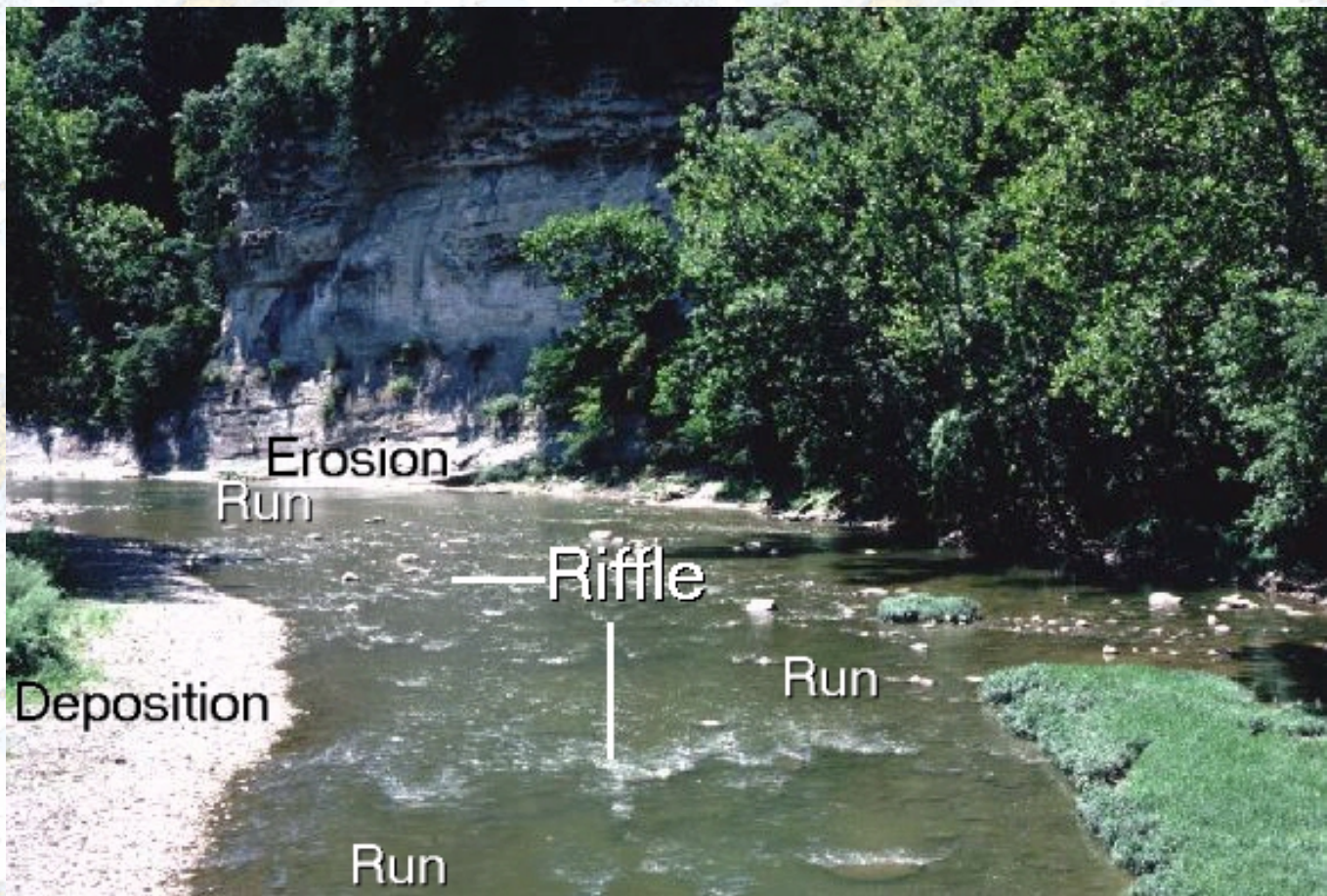


Figure 8. Habitats in a river(above). Riffles occur in shallow areas where rocks penetrate the surface of the water. Runs are deeper areas of swift current, usually upstream or downstream of a riffle. Pools are areas of still water. In rivers, erosion usually takes place on the outer edge of a bend, deposition on the inner edge. Water is usually deeper on the outer edges of a bend. The image below, of Sugar Creek in Indiana, shows a series of riffles and runs. The cobble substrate apparent in the areas with smooth surface waters suggest relatively high current velocity, thus these areas are better described as runs than as pools. Note the importance of vegetation in stabilizing a bank.



Areas of a stream may switch between being depositional and erosional as more or less water enters the stream. It is important to remember that streams are dynamic, constantly changing. Periods of high and low water may be seasonal or daily depending on such factors as climate, nature of the watershed, and the need for electricity in Las Vegas. For instance, streams in wooded areas are more resistant to flooding than streams in urban areas because the trees, with their leaves and roots, slow the movement of water, keeping it from running off and releasing it slowly; water runs right off urban streets.

Streams differ from lakes in terms of the effects of the watershed or catchment on the biological processes. While lakes are largely influenced by their catchment, they are influenced to a lesser degree than are streams, since the lakes can build up reservoirs of important nutrients and other materials. Streams, on the other hand, may rapidly lose any nutrient that escapes into the water. The fact that many nutrients are carefully conserved as they flow through stream ecosystems has opened a "hot" area of stream research into what is known as *nutrient spiraling*. Streams are often shaded by trees on the banks, and thus little photosynthesis can occur. These streams are highly dependent on outside energy sources (as distinct from the sun); this outside material is known as *allochthonous* as opposed to *autochthonous* materials derived within the stream itself. Streams are often much more dependent on allochthonous sources (such as plant leaves each fall) than are lakes. Note too that the presence or absence of trees will affect the temperature characteristics of the stream; clearcutting of forests not only increases the amount of soil that rushes into a stream, it also warms the stream up, reduces the amount of O<sub>2</sub> present, increases BOD, and so on.

As we have already mentioned, streams vary in size. Generally speaking, as a stream increases in size, it will carry more water at a higher speed, be more turbid, be deeper, and be more saline. Riffles and pools will be replaced by long runs. The progression from small headwater streams or springs to great rivers with deltas and distributaries carrying the water into the ocean, is orderly. So orderly, in fact, that a deceptively simple scheme for classifying rivers has come about (Fig. 9). *River order* is calculated as follows: The first discernible stream that forms (from a spring in most parts of the world) is 1st order. When two 1st order stream merge they become 2nd order; when two 2nd order streams merge a 3rd order stream is formed. A first order stream entering a 3rd order stream has no effect. The problem comes in when trying to pin down those first streams, which may dry up from time to time. Since river orders are usually calculated on maps, the resolution of the maps used is also critical. Generally, first order streams are the ones that show up on United States Geographical Survey 7.5° topographical maps or "quads". Drainage patterns of rivers may often be distinctive due to the underlying geology.

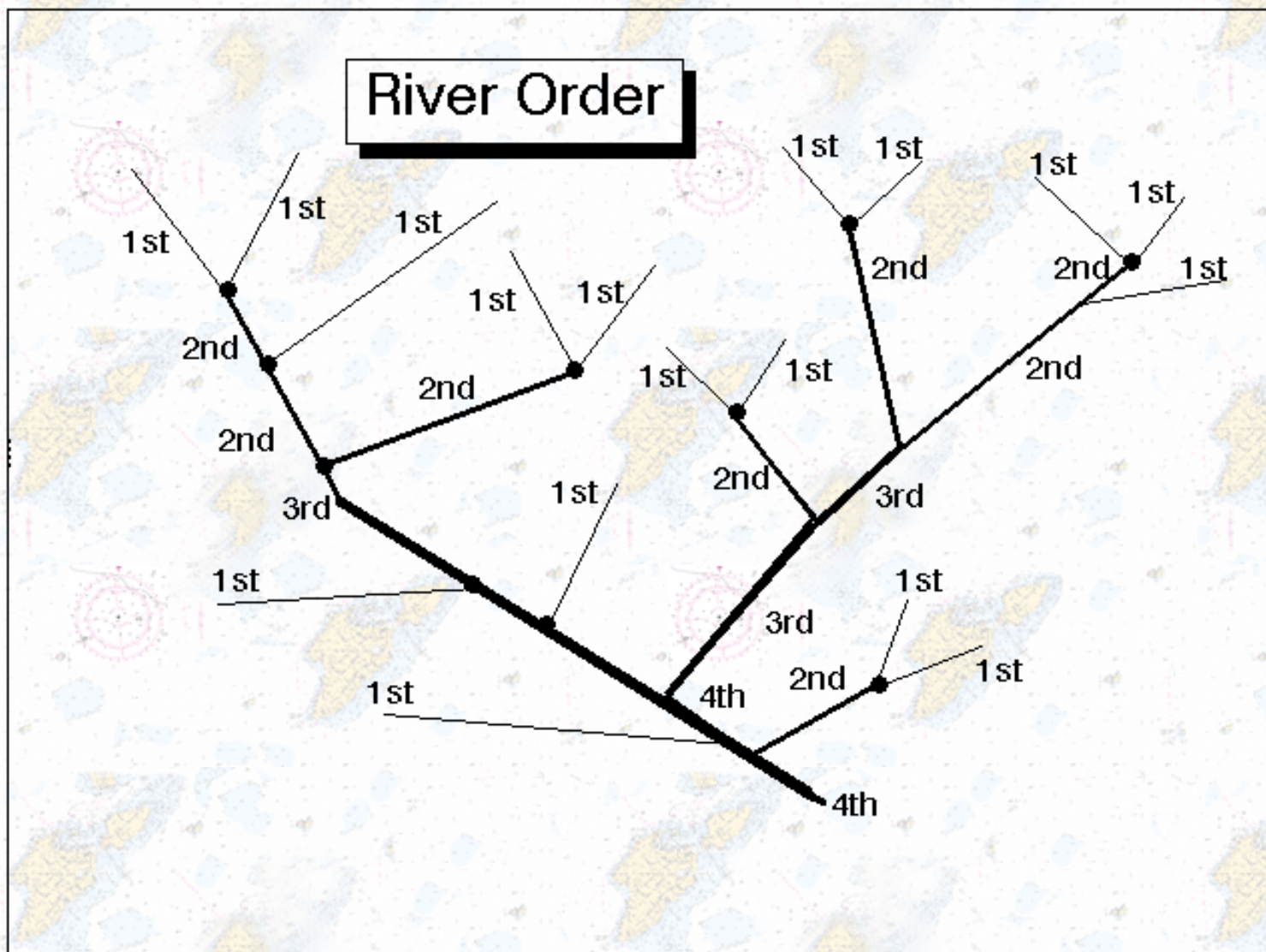


Figure 9. Determination of river order. The smallest streams are all 1st order, when two 1st order streams join they form a 2nd order stream; when two 2nd order streams join they form a 3rd order stream, and so on. Note that addition of a lower order stream does not change the order of the stream; stream order increases only when two streams of equal order join.

As you may have guessed by now, the distinction between lotic and lentic systems is very fine. One of the striking features of the natural world is its firm rebuffs to those who want to divide it up and classify it in neat packages. Most systems are not composed of discrete units but instead are continua, and the lotic - lentic continuum is one of those. As we have seen, even in an otherwise lotic system there are small pockets of calm water which are essentially lentic. On the other end of the scale, very large lentic systems can resemble lotic ones. For instance, Lake Erie is lentic, yet the western basin of the lake, which is very shallow, resembles a large river in some aspects of its biota. Many of the species present are more at home in rivers than in a lake, with the wave-swept shores being most river-like in respect to their flora and fauna.

### Marine Habitats

We have already considered many aspects of marine habitats. The open water of the ocean is known as the *limnetic* or *pelagic* zone (Fig. 10); the *oceanic* zone refers exclusively to waters not lying over the continental shelf and *neritic* refers to those coastal waters over the shelves. In the oceans, the benthic zones are the *littoral*, which here means the area between high tide and 100m deep and has nothing to do with plant life; it includes the *continental shelf*, which extends to about 100 m deep; the *bathyl* zone which extends to 2000 m (below the photic zone or LCP), the *abyssal* zone from 2000 to 4000 m, and the deep oceans or *hadal* zone from 4000 to 10,000 m.

# Zonation in the Oceans

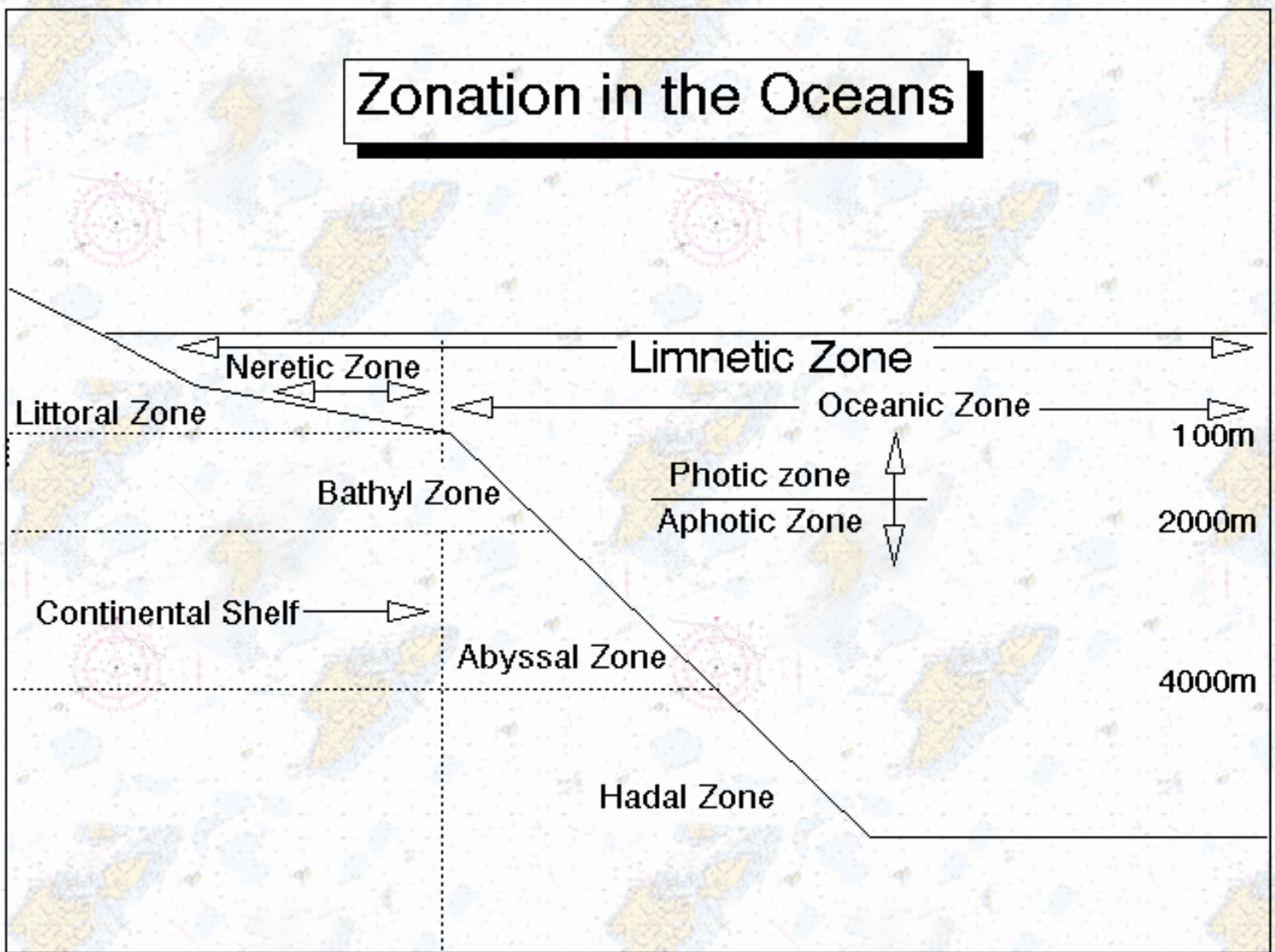


Figure 10. Habitats in the ocean. The benthic habitats are the littoral zone from high tide to about 100m, the bathyl zone from 100 to 2 000m, the abyssal zone from 2 000 to 4 000m, and the hadal zone below 4 000m. The continental shelves usually provide the bulk of the littoral habitat. The open water zones are the neritic zone over the continental shelves, and the oceanic zone over the deeper areas; together the neritic and oceanic zones constitute the pelagic zone. The light compensation point (LCP) delineates the upper photic zone from the lower aphotic zone, the depth of the LCP depends on water clarity.

As a general rule, the oceans do not stratify the way that lakes do. For a variety of reasons, the bottom of the ocean usually does not go anoxic, though exceptions to this exist, especially where human pollution is severe. In other areas, powerful currents sweep the bottom and bring in fresh  $O_2$ . Oceanic currents are caused by heating of the water at the equator; the warm water flows poleward near the surface in currents like the Gulf Stream, near the poles it cools and returns to the equator along the bottom. These currents are, of course affected by both the Coriolis force and the nature of the ocean basins. Other currents are created by the wind; for instance, strong winds blowing north along the coast of Peru move surface waters away from the coast; the surface water is replaced by nutrient rich water from below in an *upwelling current*; algae grow; small fish come to feed on the algae; and you get anchovies on your pizza. Of course, the main differences between marine habitats like the open ocean and its bottom and lakes are the salinity, the depth, and the lack of allochthonous inputs. The bottom is nearly lightless, very cold, and utterly dependent on photosynthesis in the surface waters above for any input of energy. In many ways, deep ocean habitats resemble terrestrial caves as ecosystems go.

It has been said that the pelagic ocean, from the surface to the bottom, is a biological desert. This is misleading because deserts are often rich in fauna and flora, while the analogy tries to convey the relative lack of organisms in the open ocean. The open oceans are relatively bare because of the lack of nutrients in the surface waters. The living organisms that do exist here quickly use up the nutrients that are available, and further productivity is limited. The bottom below is impoverished because of the limited productivity above. Another factor is the relative lack of any type of structural complexity in the environment; it is a general axiom that, in the absence of toxins and the presence of the essentials of life, the more complex the environment is spatially, the more species will be present.

The oceans also have several unique habitats not duplicated in freshwater. Coral reefs are among the most productive

ecosystems in the world. They are formed by precipitation of  $\text{CaCO}_3$  (limestone) from the water by small anthozoans. These structures may be only centimeters in length, or they may be thousands of kilometers in length like the Great Barrier Reef of Australia, arguably the largest artifact created by any organism on the planet. Coral reefs form only in clear, shallow, warm water. The coral polyps have endosymbiotic algae which produce much of their food; this accounts for the need for shallow (less than 90 m, corals are most common at depths less than 50m), clear water. Apparently the temperature is also critical, perhaps because of the need for high rates of calcification; reefs do not form below  $18^\circ\text{C}$ , and temperatures above  $30^\circ\text{C}$  may also have a deleterious effect. Still, this temperature and depth restriction leaves large areas of ocean, particularly in the Pacific and Caribbean, available for colonization by corals. The many types of corals which typically grow together provide a diverse habitat with many crevices and other hiding places for animals, as well as numerous sites for the growth of algae. This leads to an extremely diverse community that is becoming increasingly well studied by use of SCUBA gear. Among other things, the fact that corals only grow under certain conditions gives us important clues about prehistoric climates and sea levels; wherever fossil coral is found (and remember that coral is self-fossilizing!) there was a warm, shallow ocean.

Kelp beds form in waters too cold for coral, but kelp beds are almost as diverse. Kelp is a brown alga (Division Phaeophyta, Genus *Nereocystis*) which may reach 40 m in length, it provides a habitat for a diverse assemblage of organisms. Other types of large seaweeds such as *Sargassum* (another brown alga) or Eel Grass, or Irish Moss, etc. all form extensive beds with complex spatial habitats and a relatively high animal diversity.

Shores are another region of the ocean with a good deal of diversity. The nature of the shoreline with respect to the substrate (solid rock, boulders, cobble, sand, silt) and the strength of the waves, along with the tidal range combine to determine what sort of community will develop. Depositional, wave-washed shores of boulders or smaller debris will be too unstable for a rich community to develop in the wave zone, but in areas protected from waves, such as bays or tidal flats, diverse communities can appear, often centered around some type of vegetation such as marsh grasses or seaweeds. Rocky shores provide attachment for a wide variety of organisms, which often arrange themselves in very discrete vertical bands or strata. Rocky shores also may allow *tidal pools* to form. Tidal pools are extreme environments, yet they support surprisingly diverse communities. Submerged only at high tide (every 12 hours), tidal pools spend the next 12 hours being exposed to rapid warming or cooling, and greatly increased salinity (unless it rains). Organisms which live there must therefore be both *euryhaline* and *eurythermal*. Other organisms of the *intertidal zone*, the area between the high and low tide marks, must be similarly adapted. Of course, all of these shoreline organisms must be able to maintain a grip on the substrate in the face of storm-driven waves. Some are champions at this; the glue holding barnacles to rocks has long been a subject of study in naval research labs desperate to find a strong, waterproof glue.

*Estuaries* form where rivers enter the ocean in a protected area. As mentioned earlier, estuaries often show complex vertical zonation as waters of various temperatures and salinities mix. In addition, there are often vast beds of vascular plants in the shallow waters to provide additional habitat and cover. The varying temperature and salinity calls for adaptable organisms, and many answer the call, making estuaries another diverse habitat. An abundance of nutrients make estuaries highly productive, and the calm, sheltered waters combines with the nutrients and cover to make estuaries an important nursery area for the larvae of many species. Many of our important food fish start out their lives in estuaries. Humans also find the areas around estuaries attractive places to live, and human impacts on estuaries is severe in many areas. Protecting these crucial habitats is essential for maintaining stability in a number of marine habitats.

Perhaps the weirdest marine habitat are the recently discovered (1977) *vents* on the ocean floor. These vents form where water, heated and mineralized by contact with volcanic rock, wells up out of the ocean floor. The warm water carries a large amount of  $\text{H}_2\text{S}$  and other chemicals that *chemosynthetic* bacteria can extract energy from. These bacteria act as the base of the food chain, either by being ingested or by living as endosymbionts in other organisms clustered around the vent. A variety of worms, echinoderms, crustaceans, molluscs and other phyla cluster around these vents, where the water temperature may exceed  $200^\circ\text{C}$  (it doesn't boil because of the pressure). Obviously, these organisms have found some way to stabilize their proteins at these temperatures. Each vent is like an "island" - separated from other vents by stretches of cold, nutrient poor water that apparently forms an effective barrier to dispersal, since each vent may have a unique community formed of *endemic* (found nowhere else, as opposed to *pandemic*, found everywhere) species. You might want to read the fictional account by Arthur C. Clarke in *2010: Odyssey Two* of similar life elsewhere in the solar system.

### Some Other Aquatic Habitats

By now, you should be aware that some of the most biologically interesting habitats come at boundaries. The principle is so general that it extends to terrestrial ecosystems and even to human political systems. Mobile organisms living near boundaries can indeed have the best of both worlds. Vents, estuaries, rocky shores, all benthic habitats, the air-water interface: all of these are productive habitats located on boundaries. Before we leave the subject of habitats, let us consider a number of very small habitats often overlooked, yet extremely interesting biologically.

Temporary pools come in all sizes and shapes, but share in common the fate of being ephemeral - they dry up. Often

overlooked, they may contain a diverse assembly of living things. Many of these organisms have unique strategies that allow them to survive long periods of desiccation. These might include drought-resistant eggs or spores, the ability to burrow down into the mud and conserve water (found in lungfish and a number of amphibians), and the ability to actually dry out, yet come back to life when rehydrated (*cryptobiosis*, exhibited by tardigrades and rotifers, among others). Temporary ponds are often shallow, well-lit, predator-free, and rich in nutrients, making them favorable habitats for the organisms which can tailor their life cycles to periodic desiccation and large fluctuations in salinity and temperature. Many organisms show drastically decreased life cycle times as compared to other members of their taxon which do not inhabit temporary pools. Temporary pools normally form in depressions during wet seasons, after snowmelt, during flooding, or even just after a rainfall. The nature of the basin is variable: pockets in rock, low-lying areas, holes in tree stumps, pockets formed by leaves, and human structures such as cattle troughs, tire ruts, drainage ditches, bird baths, and so on. In fact, human-created habitats may be particularly important; some of the worst mosquito pests do their best breeding in water that collects in old tires; the tires absorb heat from the sun and form warm, sheltered habitat for the mosquito larvae. The life span of temporary pools may last from hours to months. Organisms which colonize such habitats may travel arrive as resistant spores or eggs carried on the wind or by waterfowl; they may persist in resistant stages in the soil; or they may be carried in by floodwaters. Amphibians are noted for their use of temporary ponds as breeding sites; of course the adult amphibians can traverse the terrain to deposit eggs in the temporary pond.

### Further Reading

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## Respiration in Aquatic Organisms

### The Problem

Most aquatic animals need to obtain  $O_2$  from the surrounding water in order to carry on cellular respiration. As we have seen, the amount of  $O_2$  in water is limited, and both  $O_2$  solubility and demand are correlated with temperature. At most, there is only about 15 mg of  $O_2$  per liter of water. In order to carry out the chemical reactions needed to maintain life and reproduce, aquatic organisms must be able to efficiently extract that 15 mg of  $O_2$  from the water.

The primary method of  $O_2$  transport is simple diffusion. Since all molecules are always in motion (except at 0 K), they will tend to move randomly. If they are highly concentrated in one spot, they will be least likely to move towards that spot, as opposed to moving to any of the other spots in the environment. If you divide a card deck into the red cards and the black cards, and randomly move two cards from each deck into the other, you are more likely to move red cards into the black pile, and black cards into the red pile, than you are to move red cards into the red pile or black cards into the black pile, at least until there are about equal numbers of red and black cards in both piles.

Because the speed with which  $O_2$  molecules move in water at normal temperatures is fixed, we can make some estimates over the distances at which simple diffusion can take place in both water and body fluids; that distance appears to be about 1 mm. If a cell is no more than 1 mm from water with sufficient  $O_2$ , then no special adaptations are needed for obtaining  $O_2$ . If the  $O_2$  concentration of the water is low, or if the cell is greater than 2mm in diameter, or if the organism is multicellular, with some cells buried inside the body, then special measures are necessary.

One of the simplest measures is *cyclosis*, the internal streaming of the cytoplasm of a cell. Cyclosis can help distribute  $O_2$  within a cell, but even it has limits, as we shall see. Consider what happens to a cell as it grows. If we are talking about a spherical cell, its volume grows according to the formula  $v = 0.5236d^3$  ( $d$  = diameter), while its surface area grows according to the equation  $a = 3.1416d^2$ . The volume is an index of how many  $O_2$  requiring enzymes are present, the surface area represents the "gateway" through which the  $O_2$  must pass. If the volume increases faster than the surface area - and it does, with the volume increasing by a factor of  $d^3$  and the surface area by only a factor of  $d^2$  - then the cell will soon reach the point where  $O_2$  will not be able to enter the cell fast enough. Similar arguments are used to determine the capacities of rooms with various numbers of doors when writing fire codes.

Thus we see that the problem of respiration in aquatic systems is a combination of the amount of dissolved  $O_2$  present, the distance over which diffusion can take place, and the surface area/volume ratio of the organism to be served. Taken together, these factors suggest that life in water should be restricted to very small organisms where diffusion distances are short and surface/volume ratios are high. The fact that large organisms are common in water suggests that there is a way around these restrictions, and, in fact, a number of methods are employed by large aquatic organisms to obtain enough  $O_2$ ; we will turn to those solutions next.

### Solutions

Obviously, one solution is to avoid the problem altogether. There are two basic mechanisms to avoid the problems of  $O_2$  uptake in aquatic systems mentioned above, and many aquatic organisms use both to some extent. They are to stay small and to have a low metabolic rate. Small size avoids the problems with diffusion distances and surface/volume ratios mentioned above; low metabolic rates decrease the need for  $O_2$ . Many aquatic organisms, including most larvae, are small enough that simple diffusion will suffice to supply  $O_2$ . Low metabolism is also possible, and, particularly at low temperatures, almost unavoidable for small organisms. Unfortunately, warm conditions will raise metabolism rates, often

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above levels, which can be matched by O<sub>2</sub> uptake; this, coupled with the decreased solubility of O<sub>2</sub> at higher temperatures, may define upper temperature limits for many aquatic organisms.

Problems with small size include the inability to counter strong currents, susceptibility to predation, decreased utility of predation as an energy source (it's hard to feed on organisms as big as you are; smaller ones are better), and decreased ability to control internal conditions such as osmotic pressure and temperature. Natural selective pressures for larger organisms no doubt played a role in developing some of the other solutions to O<sub>2</sub> uptake in water.

To maintain a high metabolism, or to increase body size, other strategies must come into play. The most obvious is to increase surface area without increasing volume, and there are two basic ways to do this. The first is to alter the shape of the organism. We looked at what happens with spheres, where surface/volume ratios decrease as size (diameter) increases. The same relationship holds for other shapes, but it is somewhat diminished for long, thin shapes. For example, let us consider cubes and rectangular boxes. A cube has its surface area equal to  $6 \cdot L^2$ , where L is the length of the sides, and its volume is equal to  $L^3$ . Obviously, when the length exceeds 6 units, the surface/volume ratio will be less than one. For a cube 10 units long, the surface area is 600; the volume is 1,000; and the surface/volume ratio is 0.6. Consider a rectangular box 100 units long by 10 units wide and 1 unit high. Its volume is the product of its length times its width times its height or, in this case, 1,000, the same as our cube. Calculation of the surface area of such a box is a little more involved. There are two sides with an area of  $100 \cdot 10$  or 1000; two sides with an area of  $100 \cdot 1$  or 100; and two sides with an area of  $1 \cdot 10$  or 10. Multiply and add up all the areas and you get a total surface area of 2,220 and a surface/volume ratio of 2.22, well above the value of 0.6 for a cube of the same volume.

Organisms that avoid blocky, compact shapes such as spheres and cubes, and tend towards shapes with at least one dimension greatly elongated maximize surface/volume ratios while maintaining a constant volume. This in turn allows for efficient gas exchange even without some of the additional systems we will mention below, and, as a bonus, has the effect of minimizing diffusion distances. For instance, in our cube and box, a cell at the middle of the cube would have been 5 units from the nearest surface; in the box no cell would be more than 0.5 units from the nearest surface; if the units were mm, then all cells in the box would have been able to receive O<sub>2</sub> by diffusion.

In aquatic systems, many organisms apparently optimize their shape in this way. There are flattened organisms such as the simple Mesozoa and Placozoa, Platyhelminthes, *Ulva* the sea lettuce, nudibranchs, and others. Many seaweeds and aquatic vascular plants such as *Vallisneria* have flattened blades or leaves; in fact, the leaves of terrestrial vascular plants are also examples of this phenomenon, although here the surface area is maximized to provide for light capture, not O<sub>2</sub> uptake. Other aquatic forms with large surface areas include the myriad *vermiform* (wormlike) phyla. Simple gas exchange across the surface of the body, whether the body is spherical or wormlike, is called *cutaneous uptake*, and it is an important source of O<sub>2</sub> for many organisms, even complex ones with more advanced systems as discussed below.

The other way to maximize surface area without increasing volume is to include numerous small protrusions, evaginations or invaginations on the surface of the body. This approach is also common in nature and found in the gas exchange structures of both terrestrial and aquatic organisms, and also in filtration systems, digestive tracts, and even the surface of the human brain.

Some aquatic organisms can get by simply by having bodies with numerous evaginations or invaginations. Sea anemones and jellyfish, for instance, have large spaces inside their bodies that are continuous with the outside water, and cells adjoining these spaces are thus able to absorb O<sub>2</sub> directly from the water contained there. No specialized structures are needed to move the O<sub>2</sub> around the body, and normal feeding movements circulate the water in the spaces. Most aquatic organisms, however, that rely on either basic body shape, small size, or simple evaginations or invaginations, are limited to a life with low metabolic demands. They will be sluggish, slow moving, and unable to support much in the way of nervous tissue, a notorious consumer of O<sub>2</sub>. It has recently been suggested that the dorsal nerve cord of vertebrates evolved in response to the need for high O<sub>2</sub> levels in nervous tissues; the prototypic vertebrate may have been a bottom feeder with the ventral side constantly exposed to anoxic conditions; this would have favored migration of the nervous tissue to the dorsal side (Bieri and Thuesen, 1990).

The evolution of larger, more complicated aquatic organisms capable of high metabolic rates required additional solutions to those already mentioned, although, it should be noted, the basic principles we have already seen provide the basis for the solutions employed by more complex organisms. Many of these organisms employ specialized respiratory structures called *gills*. Gills are basically areas of the body modified for gas exchange by virtue of being either highly evaginated or highly invaginated. The large surface area allows for rapid gas exchange; the only problem that remains is getting that O<sub>2</sub> to the tissues that need it. For this, many organisms have evolved circulatory systems that pump an internal fluid through the gills to obtain O<sub>2</sub> and then transport the O<sub>2</sub> to metabolizing tissue. Often pigments, probably derived from pigments used in the electron transport chain, are used to carry the O<sub>2</sub> in the circulatory fluid, or *blood*.

A basic circulatory system involves a *heart* to pump the blood and *vessels* to carry the blood. The vessels must branch enough to bring the O<sub>2</sub> within diffusion distance of any cell in the body. Most organisms use an *open* circulatory system,

where the blood is confined to vessels only part of the time, usually on the way to the tissues. After reaching the tissues, the blood drains back to the heart via *sinuses*. In a *closed* circulatory system the blood is always encased in vessels. The greater the demands placed on the circulatory system, the more likely it is to be a closed system; organisms with advanced nervous systems usually have such a system.

The pigments used to transport  $O_2$  are critical. Hemoglobin is the most familiar; it exists in a number of forms and is found throughout the animal kingdom in such taxa as vertebrates, echinoderms, molluscs, insects, crustaceans, annelids, nematodes, flatworms, and ciliates. Other pigments include *hemocyanin*, a copper-containing pigment found in molluscs, cephalopods, gastropods, crustaceans, and chelicerates; the iron-containing pigment *hemerythrin* found in sipunculans, polychaetes, priapulans, and brachiopods; and *chlorocruorin*, a third iron-containing pigment found in some polychaetes. These pigments generally bind  $O_2$  more strongly when  $O_2$  levels are high (in lungs or gills), and release it when  $O_2$  levels are low (in respiring tissues) (Fig. 1). All of the pigments exhibit the *Bohr effect*; they bind  $O_2$  more tightly under alkaline conditions and release it more readily under acid conditions. Thus  $O_2$  uptake is further facilitated in the respiratory structures where  $CO_2$  levels are low (and thus alkaline pH), and  $O_2$  release is facilitated at actively respiring tissues where there is excess  $CO_2$  and thus an acid pH. Some organisms, such as the midge *Chironomus*, use hemoglobin not so much as an  $O_2$  transport molecule as an  $O_2$  storage molecule, much the way myoglobin is used in vertebrate muscles.

## Hemoglobin-Oxygen Dissociation Curves at 3 different pH levels

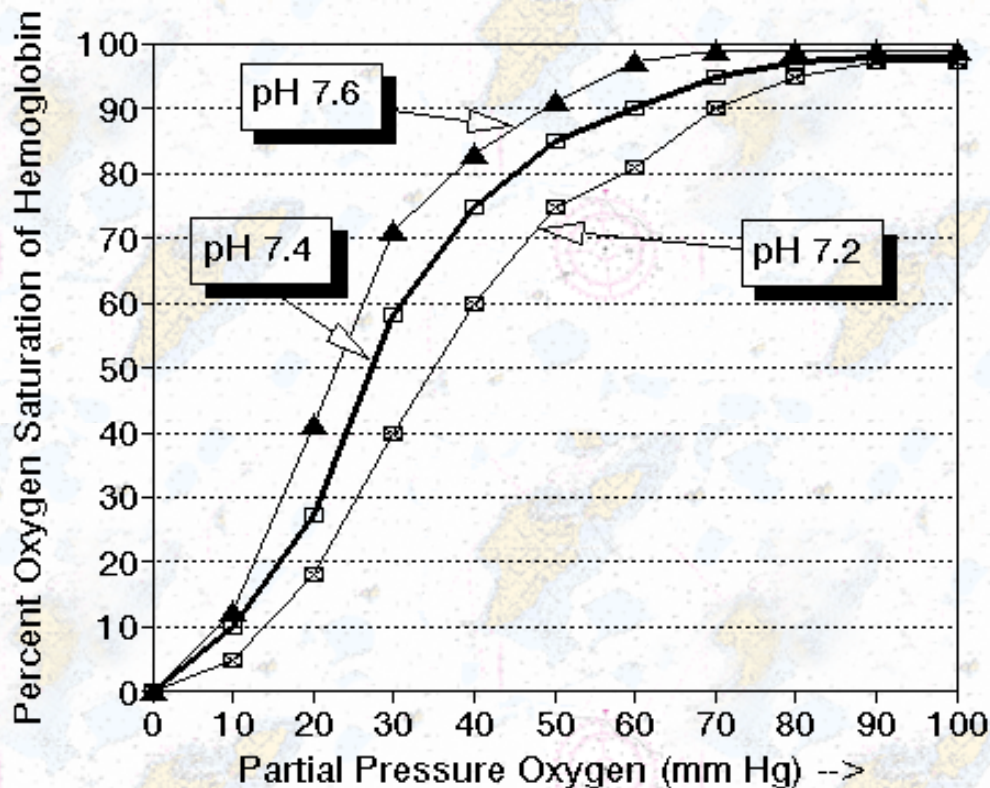


Figure 1. Oxygen dissociation curves for human hemoglobin at three different pH levels. The S-shape of the curves is due to the fact that hemoglobin begins to absorb  $O_2$  rapidly when  $O_2$  levels are between 20 and 40 mm Hg. The *Bohr effect* is illustrated here by the shift of the curve to the right as pH decreases. Of course, pH levels are high in the lungs where  $CO_2$  escapes into the air; here  $O_2$  uptake is favored. In tissues, high  $CO_2$  levels lower pH, favoring  $O_2$  release from hemoglobin. Myoglobin and fetal hemoglobin, which must take up  $O_2$  from normal hemoglobin, have curves to the left of those shown here.

Organisms with very high metabolic rates, such as fish, go to even further lengths to optimize  $O_2$  uptake from the water. One of the most elegant adaptations is *countercurrent flow* (Fig. 2). Imagine a gill as a flat plate, with water flowing over the thin surface of the plate from front to back. Along the front edge of the gill is a vein; along the back edge is an artery. Oxygen-poor blood flows into the artery at the back of the plate and flows forward through the capillaries, *counter* to the current of water flowing back over the gill. Almost immediately, the blood will pick up  $O_2$  from the water, even though the water has already lost some  $O_2$  to the gill as it flowed over it. By the time the blood reaches the vein at the front of the gill

the blood is nearly saturated with  $O_2$ , yet the  $O_2$  does not leak back to the water because the water is is saturated with  $O_2$ . If numbers help, try it like this: the water at the front of the gill is 100% saturated, grading to 20% saturated as it reaches the back of the gill. Blood at the back of the gill is 10% saturated, grading to 99% saturated at the front of the gill. At every stage along the way, the blood has less  $O_2$  than the surrounding water, so  $O_2$  always flows into the blood, never out. If the blood flowed with the water current, the blood would at best become 50% saturated, for over 50% it would start losing  $O_2$  to the water. Countercurrent flows are the most efficient way to extract something from a fluid, and we will see them again in the heat-exchange mechanisms of aquatic vertebrates and the digestive systems of many organisms.

## Countercurrent flow in gills

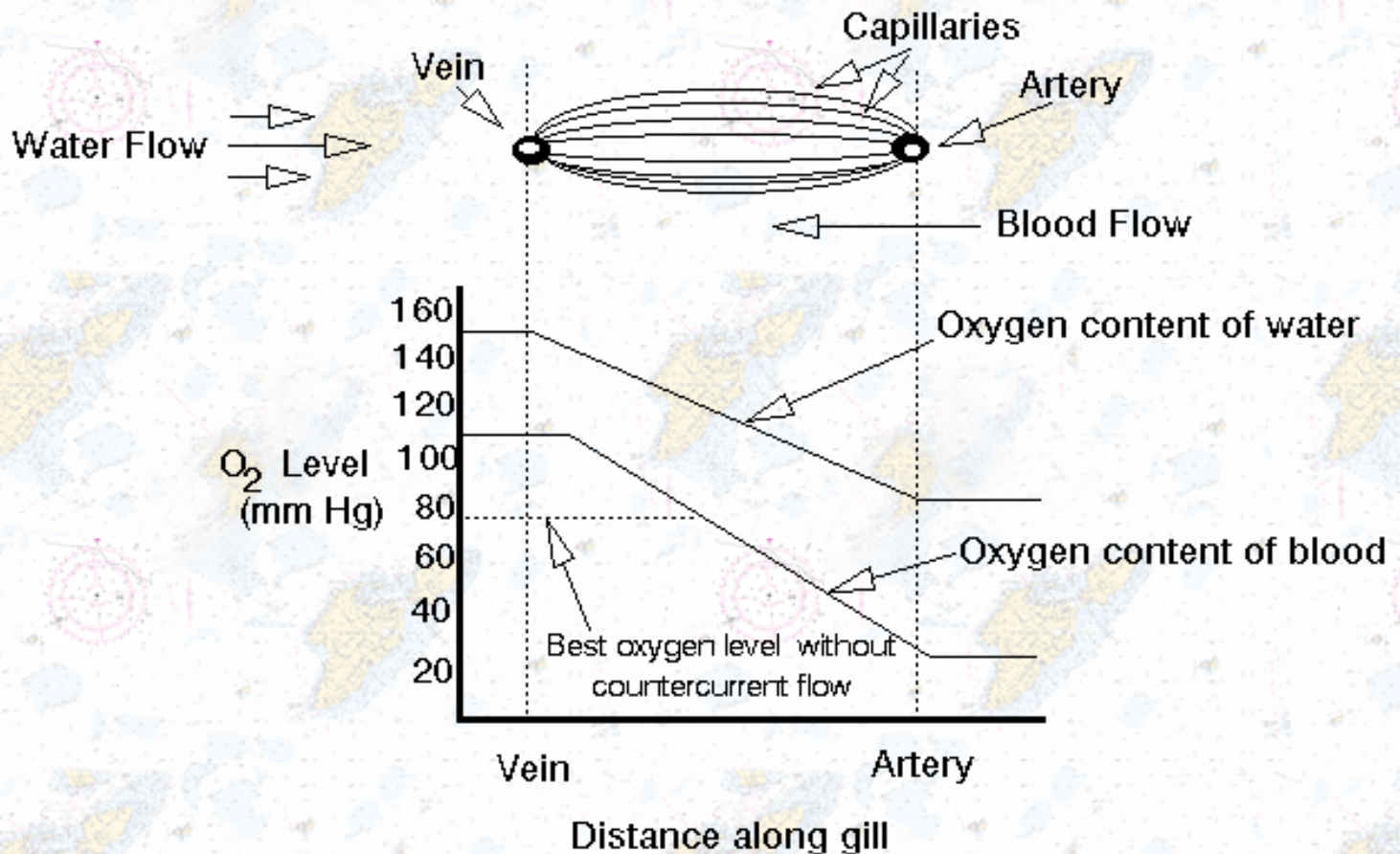


Figure 2. Countercurrent flow across a gill lamella in a fish. Deoxygenated blood flows from the artery at the posterior end of the lamella forward to the vein. As it moves forward, it encounters water moving posteriorly and will pick up  $O_2$  if the level of  $O_2$  in the water exceeds that of the blood. The countercurrent flow insures that this condition exists; the graph at the bottom shows the partial pressure of  $O_2$  in the blood and in the water at each point along the gill. Note that the  $O_2$  level of the blood is always lower than that of the water, and is in the range where  $O_2$  uptake by hemoglobin is maximized (see Fig. 1). The dotted line shows where the  $O_2$  level of the blood would equilibrate if a countercurrent flow did not exist.

Aquatic vertebrates, other than most fish, must surface to use their respiratory organs, which are adapted for  $O_2$  uptake from the air. Many fish in stagnant waters also utilize a highly vascularized portion of their gut (the precursor of the lung) to supplement  $O_2$  uptake from their gills. Common aquarium catfish that regularly rush to the surface are doing this; if you notice them rushing often to the surface you may have a problem with the  $O_2$  level in the water. Amphibians probably obtain as much  $O_2$  through their porous, thin skin as they do from their lungs; in fact, there is a family of salamanders, the Plethodontidae, which do not have lungs at all! Frogs and salamanders can remain submerged for long periods of time in water. Turtles also can remain underwater for extended periods by obtaining  $O_2$  cutaneously, sometimes even pumping water in and out of vascularized regions in the throat and rectum to increase  $O_2$  uptake. This  $O_2$  uptake is sufficient to meet metabolic needs in cold weather, such as when the animals hibernate and metabolic activity is low. Reptiles and amphibians often have ways of shunting blood away from the lungs, which are useless underwater. Diving birds and mammals must maintain high metabolic rates, but have adaptations to ensure that critical organs, such as the brain, get

enough  $O_2$ . These adaptations are even present in humans, especially human children, and explain why it is not uncommon for people to survive extended periods underwater in cold water (which slows metabolism).

One last group deserves special mention at this point, primarily because it contradicts many of the statements made so far. It is not a trivial matter, either, because this group is the most successful of the animals, the insects. While most insect larvae utilize evaginations of the body surface - gills - to respire in water, aquatic adult insects are much different. All adult insects utilize *tracheae*, air tubes that branch throughout the body and deliver gaseous  $O_2$  directly to every cell. The tracheae are connected to the outside air through *spiracles*, holes in the body sometimes equipped with a closable flap. Tracheae are tiny, and, because they are not well ventilated, would not function if they had to deliver  $O_2$  in  $H_2O$  - in other words, they must stay relatively dry to function.

How, then, do adult aquatic insects do it, that is, breathe, under  $H_2O$ ? Basically, they cheat by covering their body with hydrophobic hairs that prevent water from reaching the body or the spiracles. They trap a thin layer of air near the bodies, and thus the tracheae remain full of air also. Oxygen can diffuse into this air space and thus be delivered to the spiracles and tracheae. This arrangement is known as a *physical gill* or *plastron* (Fig. 3). The problem with this system, which is also used by aquatic spiders, is that as  $O_2$  is used up the bubble shrinks. The bubble can be maintained only in  $O_2$  saturated water; a few tiny beetle species living in cool, fast streams are the only insects that can maintain their bubbles indefinitely. All other insects must surface periodically to replenish their bubbles, and large, actively swimming insects in relatively stagnant waters do so relatively frequently. In fact, for a few species, observations have shown that such surfacing is so regular that experienced naturalists can guesstimate the  $O_2$  content or temperature of a body of water by observing how often certain species surface to replenish their air. Other insects obtain  $O_2$  by extending tubes through the water surface (mosquitoes, water scorpions), or even into aquatic plants.

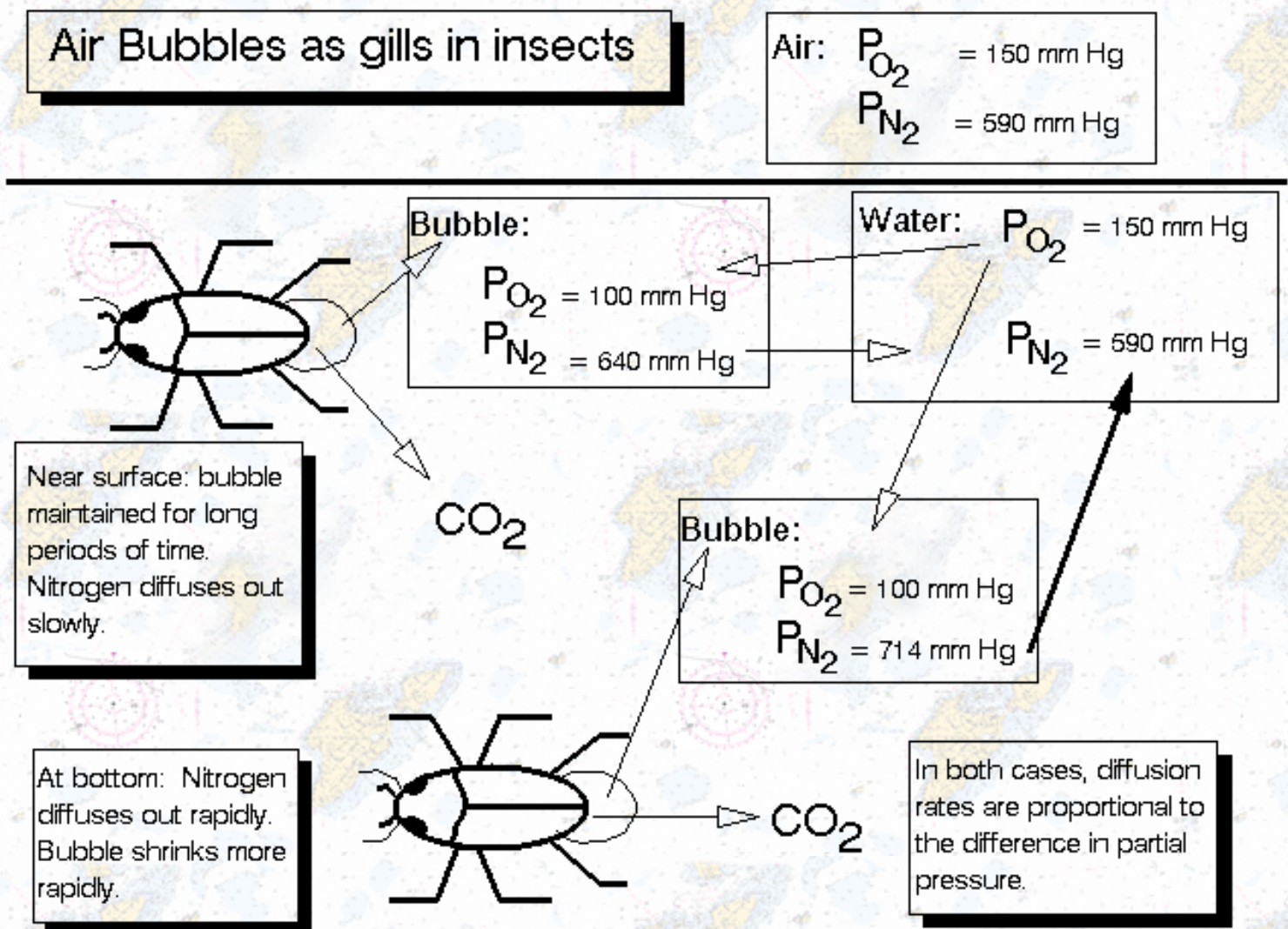


Figure 3. Operation of a physical gill at the surface and at 1 m deep. Near the surface, the bubble initially resembles the gas composition of the surrounding water.

## Aquatic Respiration

As  $O_2$  is used by the beetle, the partial pressure of  $N_2$  increases, rising above that of the surrounding water and beginning a slow decrease in size of the bubble as  $N_2$  diffuses into the water. At one meter, the partial pressure of  $N_2$  is even greater and thus the  $N_2$  diffuses into the water faster. The beetle must return to the surface as the bubble shrinks. Because  $O_2$  is removed from the bubble by the beetle, additional  $O_2$  always diffuses into the bubble.  $CO_2$  always moves readily from the bubble into the water.

Because insects use a tracheal system to move  $O_2$ , this burden is removed from the circulatory system. The circulatory system of insects is thus decidedly crude when compared to such groups as the crustaceans or molluscs with similar metabolic demands. Insects possess an open circulatory system which does not have any  $O_2$  carrying pigments; their circulatory system functions mainly to distribute food and heat.

Finally, in our discussion of respiratory systems we have ignored the problem of  $CO_2$  release. For aquatic organisms, this is rarely a problem since  $CO_2$  readily goes into solution and is carried off in the water. If there is enough surface area for  $O_2$  uptake, there will certainly be enough for  $CO_2$  dispersal. Of more critical importance is the osmoregulatory burden imposed by respiratory systems; every bit of surface area available for gas exchange is a surface that is also open to ion or water exchange; a real problem for organisms which are not isotonic in regards to the surrounding water, and the next subject we will take up.

## Further Reading

1. Bieri, R. and E.V. Thuesen. 1990. The strange worm *Bathylaelos*. *American Scientist* 78:542-549. [Read Paper](#)
2. McCafferty, W.P. 1981. *Aquatic Entomology*. Science Books Intl., Boston. 448 pp. [Read Chapter 3, pages 44-48](#)

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## Nitrogen Excretion and Osmotic Regulation

All aquatic organisms must deal with the problem of maintaining internal homeostasis, a constant internal chemical environment in which that organism's enzymes can operate efficiently. As we saw earlier, this is largely a matter of osmoregulation, but other factors are involved also. Many marine organisms can get by with minimal osmoregulation since the oceans, where the enzymes evolved, are already a good environment; other marine organisms maintain their body fluids at ionic concentrations different from the surrounding ocean and must actively regulate ions. Freshwater also calls for active measures to maintain proper osmotic balance.

One method to avoid having to deal with osmotic balance is to cover the body with an impermeable membrane. Many aquatic organisms do just that, but this protection is necessarily incomplete, because three other processes involve intimate contact between a water-permeable body membrane and the surrounding fluid. In addition, these three other processes demand large surface areas in order to occur at sufficient rates to satisfy bodily needs. These three processes are, of course, respiration, absorption of food, and nitrogen excretion. Well, actually, only respiration is required of all aquatic organisms; plants do not ingest food (although they do need to take up plant nutrients), and plants do not have to excrete nitrogenous wastes, since they possess the chemical machinery needed to incorporate N into amino acids.

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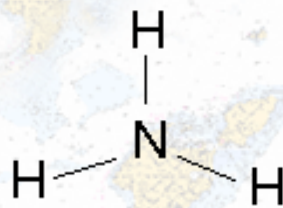
### ***Nitrogen Excretion***

We will consider the elimination of nitrogen first, a process technically known as *excretion*. Excretion is a necessary consequence of protein breakdown; when proteins are converted to carbohydrates to provide energy, the amino group is removed and must be dealt with. In the body, the amino group is quickly oxidized to form ammonia (or, at high body pH the ammonium ion). Ammonia is highly toxic and highly soluble in water. If the organism has a sufficient source of water, ammonia can simply be excreted in the water. This is the course taken by many (if not most) aquatic organisms, particularly those in freshwater. In any event, ammonia must be dealt with quickly because of its toxicity. Ammonia will diffuse passively out of respiratory structures such as gills. It takes a lot of water to dissolve and flush ammonia, however, and each ammonia molecule carries only one nitrogen.

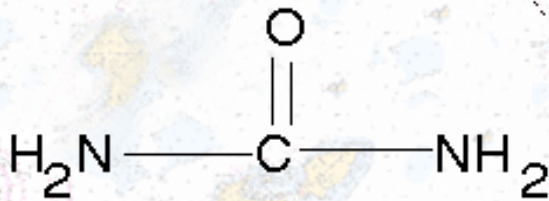
Organisms with less fresh water available, such as some marine organisms and all terrestrial organisms, are not as likely to waste water excreting nitrogen one atom at a time. They will often invest some energy to convert the ammonia into *urea*, which is less toxic, has two nitrogen atoms, and therefore takes less water to excrete. Because it is less toxic, it can be allowed to accumulate in the blood to some extent, and many organisms have specialized organs to remove urea and other wastes from the blood and excrete them. Urea is commonly used as an excretory product in vertebrates, and is rarely used in invertebrates. Some organisms, such as sharks and snails, allow urea to accumulate in their blood to help with overall osmotic balance. Sharks, for instance, use urea in the blood to make them hyperosmotic in relation to seawater, thus they tend to gain water from the ocean and do not have to worry about dehydration.

Some organisms go to greater lengths still to deal with nitrogen. Where water is at a real premium, even the low toxicity and reduced water loss possible with urea excretion is not enough. *Uric acid* is a purine even less toxic than urea, and it precipitates from solution, allowing the 4 nitrogen atoms per uric acid molecule to be excreted with just enough water so that the crystals don't scratch on the way out. It has evolved in two groups with major water loss problems - terrestrial invertebrates and egg-laying vertebrates (obviously an embryo can't just step out for a drink, and whatever it excretes is going to be very close by until hatching). Figure 1 shows the three common nitrogenous wastes.

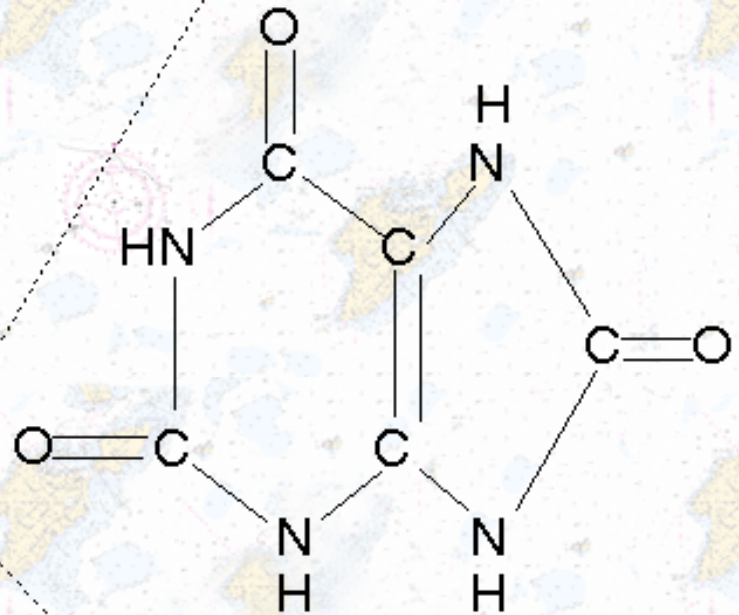
## Nitrogenous Excretory Products



Ammonia



Urea



Uric Acid

Figure 1. Common nitrogenous wastes of animals. Note that for each molecule excreted, ammonia will carry off 1 atom of N, urea 2, and uric acid 4. Ammonia is the most soluble, followed by urea and uric acid; the latter actually precipitates out of solution.

### Osmotic Regulation

With the problems of respiration and nitrogen excretion settled (we will cover feeding later), we can now deal comprehensively with the issue of osmotic regulation. First, let's review the basic situations that aquatic organisms face.

The most abundant of the salts found in the oceans is NaCl, sodium chloride or table salt. We measure salinity in terms of the number of grams of dissolved salts in 1000 g (one l) of seawater. Seawater ranges in salinity, but a useful approximation is 35 g/kg; or 35 parts per thousand or 3.5%. Places like the Great Salt Lake, certain tidal pools, etc., can have higher salinities; most freshwater systems have dramatically lower salinities.

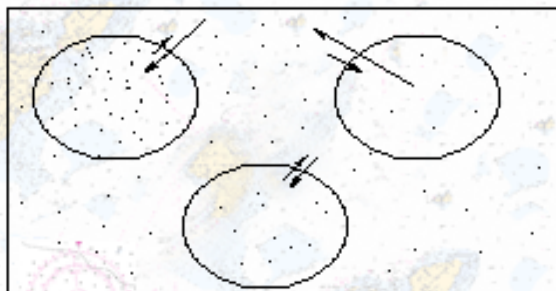
In seawater, the ions are dominated by  $\text{Cl}^-$  (19.353 gr/kg),  $\text{Na}^+$  (10.76 gr/kg),  $\text{SO}_4^{2-}$  (2.712 gr/kg),  $\text{Mg}^{+2}$  (1.294 gr/kg),  $\text{Ca}^{+2}$  (0.413 gr/kg),  $\text{K}^+$  (0.387 gr/kg),  $\text{HCO}_3^-$  (0.142 gr/kg),  $\text{Br}^-$  (0.067 gr/kg), and  $\text{Sr}^{+2}$  (0.008 gr/kg); other ions are present in trace amounts, including gold. Freshwater contains similar ions, but the amounts are highly variable and depend on season, amount of rainfall, type of rocks, etc.

Imagine water of two different salinities. We say that the more saline solution is *hypertonic* (or hyperosmotic) in relation to the other, or that the less saline solution is *hypotonic* (or hypoosmotic) in relation to the other. If the salinities were the same, they would be *isotonic* (isosmotic). Osmoticity, then, is simply a comparison of the salinities (or, more accurately, the number of dissolved particles, including non-ionic compounds) of two solutions. It is important to remember that, in considering osmoticity, that you must have two different solutions to compare - it is a relative term.

Organisms have, of course, internal osmotic levels which may differ from those outside the body. Basically, the same

three possibilities mentioned above exist, and these are illustrated in Figure 2.

hyper-osmotic hypo-osmotic



iso-osmotic

Figure 2. Three possible osmotic situations.

Organisms in marine environments tend to be isotonic in relation to the seawater. In this case, they do not have to regulate ion levels, and are termed *osmoconformers*. They are typically restricted to narrow ranges of salinity (no great handicap in the ocean, where salinity changes are not common), and are thus termed *stenohaline*. Many marine organisms, both invertebrate and vertebrate, while they may be close to isotonic, will vary somewhat and need to regulate to a small extent. These organisms will have one or more of the adaptations listed below.

Major exceptions to the above include sharks and marine tetrapod vertebrates. Sharks maintain an internal environment which is hypertonic to seawater. They raise their internal osmoticity by retaining urea in their blood. As a result of being hypertonic, they tend to gain water from the seawater through their gills and the lining of their guts. The excess water is excreted as a dilute urine.

Marine tetrapod vertebrates, which evolved on land, have blood which is hypotonic to seawater. Since they breathe from the atmosphere directly, there are no respiratory surfaces in contact with the seawater, thus reducing the surface area over which water loss can occur. Still, these organisms do lose water when excreting urea (mammals) or uric acid (turtles, reptiles, birds), and when breathing; and they gain salt ions whenever they eat or drink. The only way for these organisms to obtain water is metabolically from the breakdown of carbohydrates, and by drinking seawater. This still leaves them facing net water loss and ion gain. There are two basic solutions to this problem. Turtles and birds have special salt glands (concentrations of chloride cells) near their eyes which actively pump  $\text{Cl}^-$  ions out of the body;  $\text{Na}^+$  ions follow. Thus, birds and turtles can drink seawater and pump the excess ions out of their bodies, retaining the water. Similar cells are located on the gills of those marine fish (or invertebrates) with hypotonic body fluids.

Marine mammals have some of the most efficient kidneys known. Their kidneys can resorb most of the water from the urine, leaving a very concentrated solution of urea and salts to be excreted. They also are very efficient at removing water from the rectum, so that food wastes pass out with a minimum of water. By minimizing water loss in this way, marine mammals are able to survive on metabolic water.

Freshwater organisms (and many estuarine organisms) are hypertonic in relation to the water and thus face a constant influx of water from the surrounding hypotonic medium; they can potentially lose important ions to that solution also. Therefore, the strategy among most freshwater organisms is to cover as much of the body as possible with an impermeable coat, and leave all water exchange to a relatively small number of cells. These cells will maintain the water balance, and the remaining cells are bathed in an isotonic solution. Cells can maintain osmotic balance by using ATP to pump  $\text{Cl}^-$  ions into the cell actively. These are the same chloride cells found in the salt glands of marine turtles, they just run in reverse. The inside of the cell becomes negatively charged, and other ions, such as  $\text{Na}^+$  come in because of this. Water that flows into the body of a freshwater organism moves into the blood and excreted as a dilute urine. Freshwater organisms, because of this active manipulation of their ionic balance, are called *osmoregulators* and are frequently tolerant of a wider range of osmotic concentrations, in other words, they are *euryhaline*.

Finally, organisms in hypersaline environments such as the Great Salt Lake face problems similar to those of marine fish with hypotonic body fluids. They must actively pump chloride and other ions out of the body, and obtain water by drinking.

Chloride cells are used by both marine and freshwater organisms to pump ions. In fish (both freshwater and marine), they are located on the gills (Fig 3). Because respiratory structures must have permeable surfaces for gas exchange, they are also a common place to put chloride cells on a body which is otherwise impervious to water flow. Another popular place is in the gut and kidneys; in both places ion concentrations are manipulated to get water to flow where the organism

wants it to. Amphibians in freshwater locate these cells on their skin to absorb ions from the water. Chloride cells are also more common on organisms in habitats with changing salinity, such as temporary pools or tide pools. Aquatic mayfly larvae, which must use chloride cells on the gills (mayfly gills may be more osmoregulatory than respiratory in function) to pump ions into the body, increase the number of chloride cells as they move into more dilute water and decrease the number as the ionic concentration of the water increases.

## Osmotic Regulation in Fresh and Salt Water

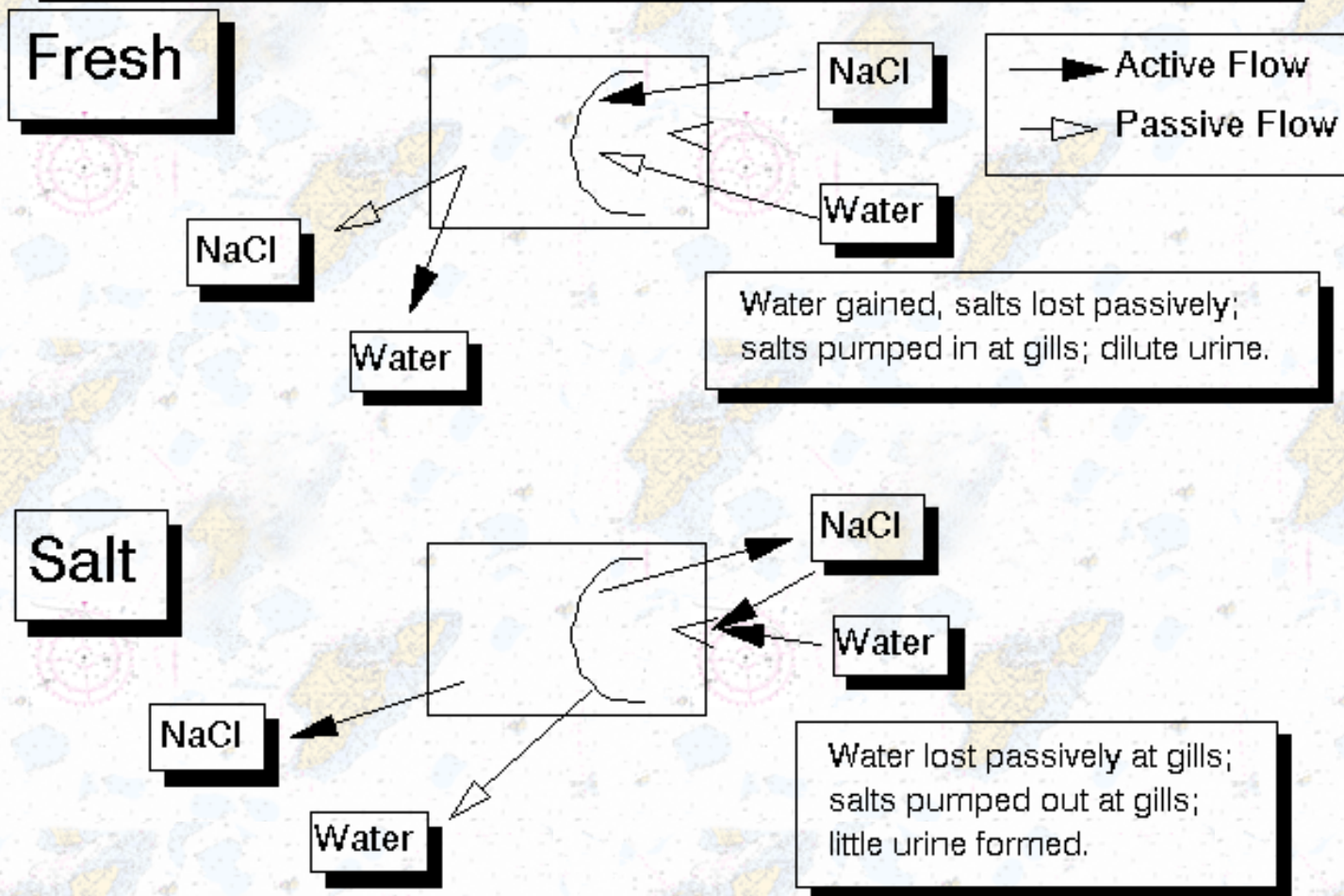


Figure 3. Diagrams of two hypothetical "fish," one in freshwater and one in saltwater. Main sites of ion exchange are the gills and the excretory organs (kidneys). Osmotic exchange also takes place across the lining of the gut (not shown here). The freshwater fish gains water but loses ions passively across the gills; to compensate, the gills actively pump in ions and the kidneys form a dilute urine. The saltwater fish gains ions and loses water across the gills; to compensate, water is ingested (along with salt), the gills actively pump ions out of the body, and a small amount of concentrated urine is formed.

### Osmoregulation and the Transition Between Habitats

As a final note, let's consider the evolutionary history of how different groups of organisms have come to colonize all the available habitats in terms of osmoregulatory adaptations.

Life originated in the oceans, and early organisms were probably isotonic, stenohaline, osmoconformers. Terrestrial arthropods, including insects, probably arose from marine arthropods which had developed water-saving adaptations in tidepools and other marginal marine habitats. Some of these organisms, i.e. insects, were later able to move into freshwater. Terrestrial vertebrates, on the other hand, no doubt arose from fish which had invaded freshwater. The freshwater fish had developed internal fluids more dilute than the oceans as a means of minimizing their osmotic regulatory needs in dilute freshwater, and the first terrestrial vertebrates, the amphibians, retained these relatively dilute body fluids. Vertebrate specialization on land required increased ability to deal with lack of water, and these water-conserving methods were useful when certain groups - marine turtles, crocodiles, birds, and mammals - returned to the sea. The main point here is that it was the osmoregulating groups that were able to colonize land, and this flexibility later allowed members of these groups to move into nearly all conceivable habitats (Fig. 4).

# Evolution of excretory and osmoregulatory strategies

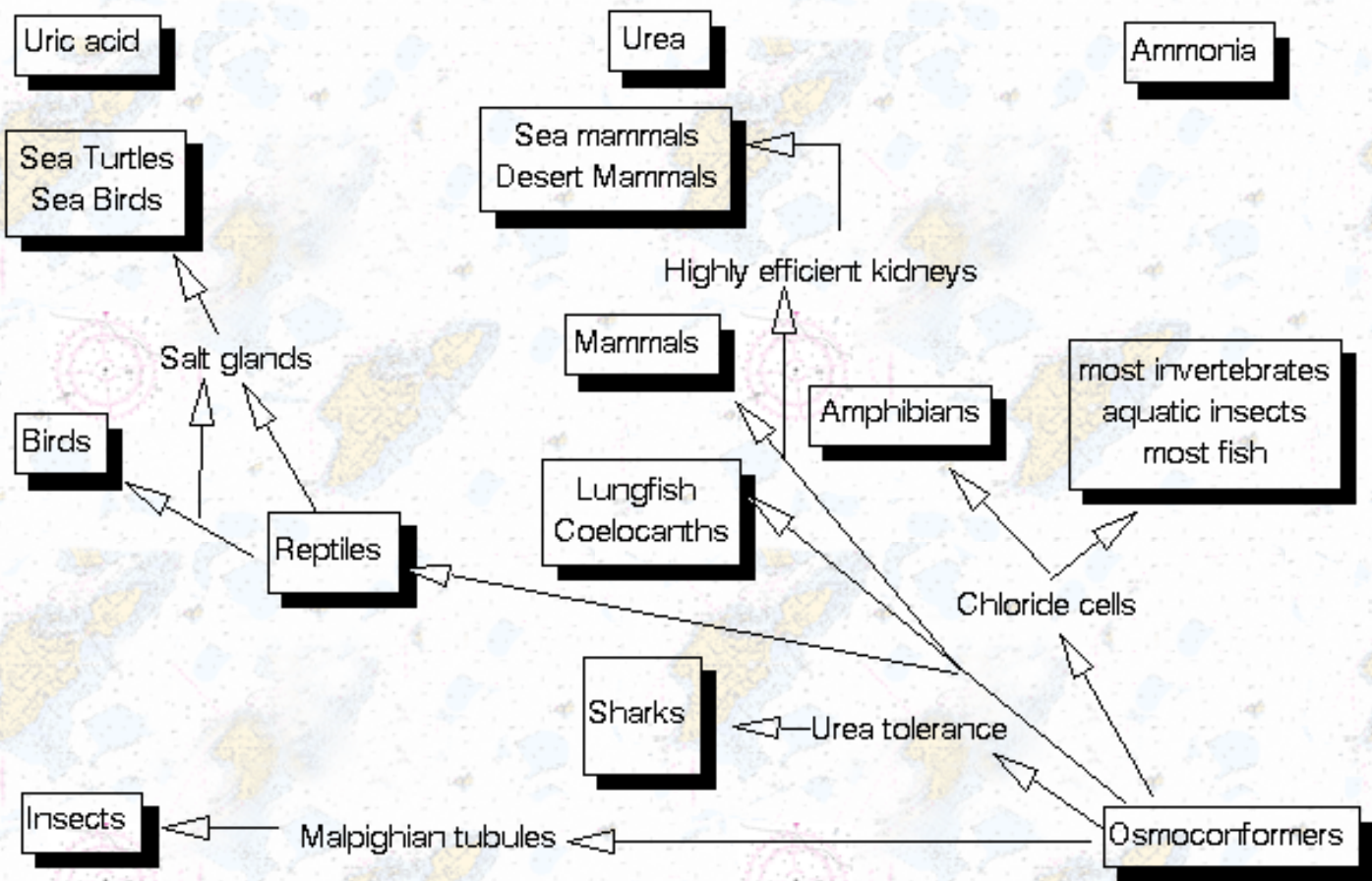


Figure 4. Major groups of osmoregulating animals and the mechanisms evolved to allow them to control osmotic levels in their habitats. Amphibians excrete both ammonia and urea; reptiles both uric acid and urea; crocodiles (not shown) excrete all three.

The failure of certain groups to make these transitions is also very interesting. Crustaceans, molluscs, echinoderms and a host of other marine groups have failed to move onto land. Those crustaceans and molluscs which have invaded terrestrial habitats are limited to moist areas, a consequence of the failure to develop efficient terrestrial respiratory structures comparable to the tracheal system of insects or the book lungs of arachnids. For the vast majority of marine organisms, however, the real problem is even deeper - the inability of the larval forms to survive in water with an ionic concentration much different from seawater. Most successful terrestrial organisms have elaborate mechanisms to protect the relatively delicate embryos from osmotic stress, while similar mechanisms are lacking for most marine phyla.

## Further Reading (Osmoregulation)

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## Locomotion in Water

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First, get a rubber band.

Movement is by no means a given for aquatic organisms. Many organisms are *sessile* for all of their lives. Some divide their life cycles into sessile and motile stages, and still others must remain constantly in motion. Some organisms move actively, expending energy to impart motion, while others drift passively, relying on water or wind currents, or density differences, to carry them. Many organisms, such as the plankton, are able to move their bodies within the currents they find themselves in, but are unable to oppose those same currents and move independently of them. The topic of aquatic locomotion is complex, and we will only be able to deal with a portion of that complexity here. We will start by examining the Newtonian physics that describes the rules of motion; then we will review some of the physical properties of water that have an effect on locomotion in the aquatic realm; and we will finish by examining the main modes of locomotion used by organisms ranging in size from microscopic plants to blue whales, the largest organism to have ever lived.

## Newton's Laws and Basic Units

Three of Newton's "Laws" of motion will suffice for our understanding of locomotion. These are: I. a body at rest stays at rest unless acted on by a force; II. a body in motion continues in a straight line unless acted on by another force; and III. for every action there must be an equal and opposite reaction. Taken together, these laws can be restated as the principles of inertia and momentum. Before going further, we have to also consider the basic units of measurement that scientists employ to express Newton's Laws mathematically.

We must first define four basic quantities from which we will derive all the other properties of objects in motion. The four basic quantities are *length*, *mass*, *time* and *temperature*; which we measure as meters (m), kilograms (kg), seconds (s) and degrees Kelvin (K) respectively.

We can now answer a number of questions concerning the organism about to go into motion. We can measure its length (or width or height) in meters and its weight in kilograms. We can go a little further, and by multiplying and adding specific measurements of its size in meters, we can calculate its surface area in meters squared, or its volume in meters cubed. All of these are pure measurements with only one of our basic units involved at any one time. We can also describe some *derived units*, which call for measurement of more than one of the basic quantities at a time. For instance, we can determine the mass in kilograms and calculate volume in terms of meters cubed, and come up with density, which is kilograms per meter cubed.

Pure units describe our organism only at rest; once set in motion, we must necessarily use derived units to describe our organism because motion requires that we keep track of how far (meters) our organism moves and how long (seconds) it takes to get there. The basic unit of motion is speed, or *velocity*, which is expressed as length/time or meters/second. We can also talk about *acceleration*, which is the change in velocity over time, velocity/time or meters/second/second. If the change in velocity is from a higher velocity to a lower one, we speak of negative acceleration or *deceleration*.

We were able to describe velocity and acceleration by using only two basic units, length and time. Other derived units bring mass into the picture. You know that catching a softball is different from catching a hardball, mainly because the softball weighs more. This introduces the concept of *momentum*, which is the product of mass times velocity or kilograms x meters/second. By itself, momentum is kind of an abstract thing; we are more interested in what it takes to get that mass up to the velocity we are interested in, or what kind of wallop, or impact, that softball will have when it suddenly decelerates in our mitt. The push or impact is another derived unit, *force*, which is defined as mass times acceleration, or kilograms x meters/second x second. This formulation is both awkward to say and useful to know, so it is given its own unit in the SI, the *newton*.

Now, it's one thing to know how many newtons it will take to get a 1.5 kg squid moving 3 m/s in 4 seconds (1.125 newtons), but it's also good to know how much energy an organism invests in locomotion. This is the realm of *work*, which is the product of force times the distance it is applied over, or length. In SI units it comes out kilograms x meters x meters/seconds x seconds; another mouthful given its own SI unit, the *joule*. If you keep track of how long you apply power, the next unit to appear is the *watt*, which is joules/second or kilograms x meters x meters/seconds x seconds x seconds. Another way to look at these units is to consider joules as energy and watts as energy expended over time. In this light, many relationships can be seen. A 60-watt lightbulb uses 60 joules/second, one calorie is 4.2 joules, one horsepower is 746 watts; to run a horse for an hour takes 0.746 kilowatt-hours or 2.6856 megajoules or 639,429 calories or 639 dietetic calories.

Finally, let us consider one last, special case of acceleration. Gravity is the force that attracts two bodies, and the Earth, acting as one of those bodies, attracts 1-kg bodies on its surface with a force equal to 9.8 newtons. We speak of the *gravitational constant* (for the Earth) of 9.8 m/s<sup>2</sup>, that is the acceleration due to gravity. The *weight* of an organism is equal to the force it applies to the ground; a one-kg organism has a weight of 9.8 newtons. Remember that the kilogram is a unit of *mass*, not weight! Weight is simply the measure of the Earth's attraction for an object, and since that relationship is proportional to an object's mass, our systems of scales utilize that relationship to *estimate* mass by calculating weight.

## Physical Aspects of Moving through Water

When an organism moves through water, there are two basic forces it must overcome. As we have seen, for aquatic organisms the force of gravity is a minor concern. Because organisms are mostly made up of water, their weight is largely offset by the weight of the water around them. Organisms that want to maneuver vertically usually have body densities approaching *neutral buoyancy*, that is, the density of the surrounding water. Organisms that want to remain on the bottom have very dense bodies (*negative buoyancy*); those who wish to remain near the surface have less dense bodies (*positive buoyancy*).

The other force that organisms wanting to move (or stay still in a current) have to contend with is *drag*. Drag, as we saw earlier, is the force imparted by a moving fluid (or the force needed to move an object through a stationary fluid); drag has two components, *friction drag* and *pressure drag*. Friction drag may be visualized as the force needed to overcome the inherent cohesion of the water molecules; pressure drag may be visualized as the force needed to push the water molecules out of the way. These two types of drag differ in their importance. Smaller organisms or slower speeds shift the emphasis to friction drag, which is proportional to wetted surface area; larger organisms or higher speeds will emphasize the importance of pressure drag, which is proportional to volume and shape.

The *Reynolds number* determines which type of drag is more important given the conditions. At  $Re < 1$ , friction drag predominates; at  $Re > 1000$ , pressure drag is the major component of overall drag; the area from  $1 < Re < 1000$  is a transitional zone where neither factor can be ignored. The formula for  $Re$  is:

$$Re = \frac{\rho l U}{\mu}$$

Where  $\rho$  = density of the fluid;  $l$  = characteristic length of the object;  $U$  = the speed (of the object or the fluid or both); and  $\mu$  = the dynamic viscosity. The length is somewhat arbitrary; it is usually the length normal to the flow, i.e. the diameter of a sphere, the diameter of a cylinder normal to the flow, the length of a cylinder parallel to the flow. Now, another way of looking at  $Re$  is in terms of its basic units. In the numerator, we have density (kg/m<sup>3</sup>), length (m), and velocity (m/s); in the denominator we have viscosity, which is the momentum of the water (kg/m·s). Multiplying across the numerator, kg/m<sup>3</sup> \* m \* m/s, we get kg/m·s, and these units cancel with the kg/m·s in the denominator, making  $Re$  a dimensionless index.

The type of drag that predominates can have dramatic consequences for the organism. For instance, we live in a world dominated by pressure drag, and the way to reduce pressure drag (thus increasing efficiency of locomotion) is to *streamline* an object, making it present a small profile to the fluid the object is moving in - a Corvette has less pressure drag than a Mack truck, even if both were the same size. However, streamlining also increases friction drag. In our world of big things and high speeds, friction drag is by far the smaller coefficient of overall drag and can be ignored, but many small organisms live under the reverse conditions and cannot afford to overlook friction drag.

Organisms give us many clues about their lifestyles with the forms of their bodies, and this is particularly true in locomotion. One look convinces us that the streamlined squid is a faster swimmer than the bulky octopus; the squid's body is adapted to life at higher  $Re$ . We must be careful with this predictive tool, however, since other factors may also enter in. In particular, it is important for us not to be prejudiced about how we view the world of very small organisms, extrapolating our own experiences with water at our scale down to microscopic scales. To microscopic organisms, water (or even air) is more like molasses. The weight of individual molecules begins to have a measurable effect, for instance,

the phenomenon called *Brownian motion*, where small particles vibrate randomly, is caused by an imbalance in the number of molecules vibrating into the different sides of the particle. We would laugh at people trying to propel themselves through water by wriggling a length of rope, yet at small scales flagellar movement is quite effective.

## ***Movement by Microorganisms***

Almost all movement by organisms (aside from moving with currents or gravity) is ultimately performed by using ATP to alter the shape of protein molecules in such a way that the protein molecule moves. The actions of thousands of protein molecules in concert magnifies the movement enough to do usable work for the organism, whether that be flexing a muscle, moving a flagellum, or moving a chloroplast along a microtubule.

Flagellar propulsion (we will, for now, consider flagellar and ciliary movement together, with some distinctions to follow shortly) is one of the simplest means of propulsion used in aquatic systems. Organisms from bacteria to flatworms use it to move the whole organism through the water, and even large multicellular organisms are not above using cilia to create currents in respiratory and digestive tracks. The differences between prokaryotic and eukaryotic flagella need not bother us here; we will concern ourselves only with the final result.

Flagellar propulsion works in a manner counterintuitive to us. Rather than acting by moving water in a rearward direction, and pushing the organism forward (from Newton's third law), the flagellum acts because as it moves the drag on one side of the flagellum is different than on the other side. Basically, what happens is that anytime a cylinder is moved with respect to a fluid at any angle other than straight, a force is developed that pulls it to one side, and that force is what is exploited for locomotion. In the case of short cilia, where the wavelength of the cilium is less than the wavelength of the motion imparted to it, the force is at a 90° angle to the cilia when it stands straight up. On a flagellum, where the ATP induced motion forms a wave shorter than the long length of the flagellar fiber, the force is either towards or away from the base of the flagellum.

Organisms typically have four or fewer flagella, usually just one. On organisms with flagella, the flagella usually make a rotating motion, much like a corkscrew, and either draw the organism forward or push it forward from behind. Organisms with cilia typically have many more - often thousands - and each cilium is much shorter than the typical flagellum. The cilia beat in coordination with each other, much like 'the wave' at a stadium. Often the cilia are arranged in discrete bands, which in turn offer more control. For instance, if the cilia on one side of the organism beat 'forward', and on the other side they beat 'reverse', then the organism will spin quickly. Usually flagella are found on smaller organisms and cilia on larger ones, and where these size ranges overlap the ciliated organisms are much faster, indicating that they are potentially the more efficient system (neither is very efficient, though). Cilia and flagella are ideal for small organisms moving relatively slowly; they require no elaborate muscles and skeleton. They only work at very low Re, however, and would be extremely inefficient on something like a whale. If nothing else, consider the old problem of decreasing surface/volume ratios as size increases. Remember that mass - one of the prime factors in determining how much force will be needed to set an object into motion - will increase with volume, and that the propulsion system, the cilia, are limited to the surface for attachment. Hydrodynamics aside, large organisms cannot use cilia or flagella as means of propulsion simply because they do not have enough surface area to attach enough cilia to move the increased mass.

## ***Movement by Macroorganisms***

With cilia not suitable as a propulsive force for larger (<2mm) organisms, some other method must be found. As we saw, part of the problem with cilia is due to the old problem of surface/volume ratios. Consider muscles, however. The fibers making up the muscle and doing the work are a large portion of the volume, and thus increase along with the size of the organism. Of course, muscles also bring on problems, such as a greatly increased need for O<sub>2</sub> and nutrients; muscles that are in action for long periods of time require efficient circulatory systems.

Take a rubber band and stretch it. The force resisting you is comparable to that of contracting muscles - exactly comparable to the muscles in your arms that are stretching the rubber band. Now let go of both ends at the same time. Is any useful work done? Stretch the rubber band again; hold one end against your leg; and let go the other end. The impact you felt was some useful work (it woke you up, didn't it? - if you were sleepy enough to follow those instructions you needed it). More to the point, shoot the rubber band across the room at your roommate or a librarian or whatever. Now you have locomotion.

For a muscle to do any useful work, it must be anchored against something. That something is usually a *skeleton*, which come in three basic flavors: *hydrostatic* skeletons, where the muscles act against pressure imposed on body fluids (by other muscles); *endoskeletons*, where the skeleton is internal to the muscles; and *exoskeletons*, where the skeleton lies outside the muscles. Of course, some organisms use these in combination, and there are a few places where no skeleton at all is used, but rather the muscles work as *antagonists* against each other. This latter situation occurs in a number of situations, from flatworms to mollusk feet to human tongues (you didn't think there was a bone in there did you?).

Reportedly, politician's spines also work on this principle. Even where skeletons exist, antagonistic muscles are often found, with one muscles responsible for movement in one direction, and the other muscle responsible for movement in another direction. The need for antagonists is a natural consequence of the fact that ATP induced contraction of muscle fibers is a one-way affair. The antagonist, by contracting, stretches its partner back out so it can contract again. In many situations, of course, gravity may also act as an antagonist.

Hydrostatic skeletons are common among aquatic invertebrates. In its basic incarnation, the fluid-filled body cavity is put under pressure by the contraction of muscles around the body cavity. When these muscles attempt to contract against the incompressible body fluids, the result is a rigid sac that forms a useful base for the muscles attached to it. A familiar example of the rigidity afforded by a hydrostatic skeleton is a balloon; it starts out limp, but once enough air is added, the rubber encircling the air space stretches and puts the air under pressure, forming a rigid structure. I'm sure you can think of other common examples of this principle.

Locomotion generally takes advantage of Newton's third law: for every action there is an equal and opposite reaction. In most cases, the action takes the form of pressing backwards against the substrate or water, with the reaction being forward movement of the organism. The points at which that backward pressure is applied are known as *pivot points*. On many substrates, the force that the organism exerts is minuscule compared to the mass of the substrate, and the substrate does not move; in these cases all of the force is used to move the organism forward and locomotion is very efficient. In loose substrates, or in water, the pivot points are on media that "give" and move backwards, wasting some of the energy and making locomotion less efficient. It is harder to run in deep sand than on gravel or a hard surface in large part because part of your effort goes to moving sand rather than your body.

Hydrostatic skeletons also make use of pivot points. We will look at several examples; the first is that of the nematode worms. These simple animals are only capable of thrashing back and forth. This motion throws their bodies into wriggling S-curves, but is highly inefficient for locomotion. As you recall from our discussion of flagella, when a cylinder is moved through water, there is more drag on one side than on the other, and the resulting imbalance of force can be used for propulsion. The flagellum is anchored to a larger body, however, and the forces can be resolved to do useful work. In the nematode, the cylinder is the body, and the drag forces largely cancel each other out, with only a small net movement resulting from thrashing around. On or in a substrate, however, efficient pivot points can be set up on the outside curves of the 'S'; and the body can thrust back against these points to move forward. It's still not very efficient, though.

Other organisms making use of hydrostatic skeletons include the segmented annelid worms (like the earthworm). These organisms have divided their hydrostatic skeleton into many small parts - one for each segment. This allows some parts of the body to be rigid while others are relaxed. It also allows for parts of the body that are relaxed to be wider than parts where the circular muscles are contracted. The combination of circular and longitudinal muscles allows for great control of the body (and requires a more advanced nervous system). It allows for more efficient locomotion, both in the pivot-crawling (described above for nematodes) and in thrusting, where one portion of the body is narrowed by contractions of circular muscles and forced forward through the substrate, where it subsequently anchors itself by expanding as a result of contraction of longitudinal muscles.

Marine polychaete worms (a type of annelid) are optimized for locomotion on or near the ocean bottom. They have the sides of each segment expanded into lobes or *parapodia*, which act as paddles when the worm swims. A paddle makes a more efficient pivot point in water since its wide end presses against a greater mass of water than a cylinder would. With these more efficient pivot points, these worms can swim. They actually form two types of pivot points - each individual parapodium forms its own pivot point, which it presses against as a result of local contraction of longitudinal muscles, and the outer curves of the body, which assumes a sinusoidal shape when swimming, also form pivot points. When crawling, the individual parapodia press against the substrate, and the worm can also twist its body, moving the parapodia rapidly.

Another type of locomotion frequently performed by organisms with hydrostatic skeletons is a looping motion. Perhaps the most familiar example of this is the motion of the inchworm (which has an exoskeleton); looping motions are also performed by *Hydra* (no skeleton) and starfish (endoskeleton), as well as cheerleaders (endoskeleton, usually double-jointed). For our purposes though, the leech is most instructive. The leech has taken a different approach to locomotion than its kin the earthworms and polychaetes. Leeches have abandoned segmentation and gone back to a more "primitive" body arrangement with a single internal cavity. They have then taken this simple body plan and combined it with suckers on either end of the body so that when it plants a pivot, it *really* plants a pivot. Leeches can also swim (not very efficiently) by waving their flattened body and forming pivots on the outer edges of the curves against the water. We will come back to the concept of undulating a flattened body to propel oneself later.

A final type of propulsion, before we leave hydrostatic skeletons, is *jet propulsion*. It operates by actively pushing water from inside to the outside in a narrow stream or *jet*. Since the water has mass, the body will acquire a momentum equal to that of the mass of the water times its velocity. It should be obvious that even a massive organism can achieve jet propulsion with a relatively small amount of water if it can accelerate that water to high velocity; you already know that the effort required to hold a hose nozzle is proportional to both the velocity and volume of water that is exiting the nozzle. Keep in mind also that as an organism squirts out water it is decreasing its own mass, making such a simple system a rather complicated one to model mathematically. Jet propulsion is found among animals with hydrostatic skeletons,

internal skeletons (squids), external skeletons (dragonfly larvae, scallops), and no skeletons (jellyfish).

Before discussing propulsion in organisms with exoskeletons and endoskeletons, we should go to the old chore, repeated in every biology course that deals with animals (and even, by habit, in some botany courses) of explaining the differences between the two. For the millionth time, exoskeletons have a mechanical advantage only for smaller organisms, where they can serve as both support and protection. Because the muscles are on the inside, they are limited as to the amount of space they can occupy, and they cannot gain leverage in their attachments. To increase the size of the muscles, you must increase the size of the tube (skeleton) which holds them, but as you increase its size you must also increase its thickness to support its own weight. The increased weight of the skeleton offsets any additional power obtained from the larger muscles. It's really a variation of our old friend surface/volume ratios in a slightly different form. Internal skeletons place no constraint on the size of the muscles, which can grow as large as necessary and which also may find more advantageous positions to attach; positions that increase leverage and thus amplify the power of the muscle. The practical limitations of each type of skeleton are obvious to us; the largest practical size for an external skeleton is about the size of the largest invertebrates in the water (30-kg lobster today, larger fossils in the past). The water supports some of the weight of the exoskeleton; larger organisms on land all have endoskeletons.

The basics of locomotion are the same for organisms with exoskeletons and endoskeletons, and we will consider them both together. In general, these can be divided up into movements of the whole body, such as pivot-crawling or pivot swimming, looping, and jet propulsion, which we have discussed above, and movements performed by the limbs which skeletons make possible such as *rowing* (a type of swimming), *walking*, and swimming by lateral undulation, which differs (somewhat) from pivot swimming.

Walking is only done by the densest aquatic organisms. It's not that they're stupid, it's just that walking requires pivot point maintained by friction, and friction requires weight (in a current, some organisms substitute drag for weight, see McShaffrey and McCafferty 1987). Walking involves a complex set of movements that must be carried out in sequence by several different sets of antagonistic muscles. First comes *elevation*, where the leg is lifted; next is *protraction*, moving the limb forward; followed by *depression*, lowering the leg to the substrate and establishing a pivot; and finally there is *retraction*, where the body is swung around the limb with the new, forward pivot point, thus moving the body forward. The coordination comes in keeping the legs from tangling with each other and making sure that retraction only occurs on those limbs that have just placed forward pivot points. Aquatic insects, for example, lift three legs at once, two on one side of the body, and one on the other. The other three legs thus form a stable tripod for the insect to rest on while the three lifted legs are protracted and depressed. With all six legs back on the substrate, the insect then lifts the three legs that hadn't been in the air, and while they are lifted, the other three legs are retracted, allowing the body to move forward. This forward movement also insures that the legs in the air will establish new pivot points even further forward.

Rowing is a very common form of propulsion among aquatic organisms with limbs, including insects, crustaceans, fish (using the lateral fins), amphibians, reptiles, birds, and mammals. Laypeople refer to it as swimming, but it is very distinct from the swimming we will take up next. Rowing is much like walking, the limb is moved forward, places a pivot, and is moved backward. The big difference is that using water as a pivot point means that rather than the limb being planted firmly, it will move backward, carrying the water along with it. It is the momentum of this moving water that constitutes the Newtonian action; the reaction is the forward momentum of the organism.

For rowing to be efficient, the backward motion of the limb (*power stroke*) must move more water than the forward motion (*recovery stroke*). For most organisms this all occurs at high  $Re$ , and here the answer is obvious to us. The limbs of rowing organisms are usually paddle-like, wide in one dimension, narrow (streamlined) in the other. On the power stroke the wide dimension is pressed against the water; the extreme drag of this configuration causes lots of water to move along to the rear with the limb; therefore moving a large mass of water rearward with the equal forward force applied to the mass of the organism. On the recovery stroke the paddle is rotated or *feathered* (for you rowing fans) and the streamlined edge moves easily forward through the water, bringing little water along with it and thus minimizing the rearward force applied to the organism. Examine rowing organisms closely and you will note flattened hind legs on beetles, collapsible fins on turtles, frogs, fish and fowl (not to mention platypuses), or even the streamlined shape of bird wings (penguins fly, or row, underwater with their wings).

At low  $Re$ , the same basic concepts apply, but streamlining is no longer effective. Small organisms typically use hairs rather than solid structures to make up their paddles; the hairs can be folded to reduce drag on the recovery stroke and do not create as much friction drag on the power stroke as a solid structure would. The physics of flow at low  $Re$  suggests that as far as rowing is concerned, a series of hairs moves water backwards as effectively as a flat plate would anyway, since water does not tend to flow between the hairs at low  $Re$ . This explains the hairs on the back legs of beetles (which are small enough to be in the transitional zone), and on the legs, antennae, mouthparts, etc. of small aquatic crustaceans.

*Undulatory swimming*, as exhibited by fish, salamanders lizards, snakes, cetaceans, and some worms, is a refinement of pivot swimming. In undulatory swimming, *thrust*, or a forward force, is generated by pushing against pivot points in the water in a highly coordinated, stereotypic pattern. The body of the organism is bent to form moving waves, and the length of the body involved has an impact on the swimming motion that will result. Long flexible fish like eels, or aquatic snakes, involve most of their bodies in the undulations and their swimming style is referred to as *anguilliform*; some fish keep most

of their body rigid and flex only the tail region in what is known as *carangiform* swimming; and others flex only the tail itself to perform *ostraciiform* swimming movements (Fig. 1). As a general rule, the less of the body involved in the swimming stroke the more effective it will be; therefore the carangiform and ostraciiform movements are more efficient because less of the body is involved (and creating drag on the recovery stroke), also, in carangiform and ostraciiform swimming certain hydrodynamic factors such as angle of attack can be optimized.

The fastest fish are those which have powerful muscles in the body coupled through a small peduncle (the base of the tail) to the tail fin, which provides most of the propulsion. This is the case for such fish as the tuna and swordfish, and also for dolphins and whales. Remember that the undulatory movements of fish are lateral and the movements of marine mammals are vertical; both are about equally efficient; the vertical movements of the marine mammal's tail are a result of the tetrapod ancestry, not some obscure hydrodynamic principle. In most fish, the *caudal*, or tail fin, provides most of the thrust, while the dorsal and ventral fins provide control over side-to-side motion or *yaw*; the lateral fins (corresponding to the appendages of a tetrapod, the pectoral and pelvic fins) provide control over rolling movements as well as the attitude of the body (head up or down, *pitch*). In most fish, rowing movements by the lateral fins provides slow-speed movement with great control, and in some fish undulations of the dorsal and/or ventral fins also provides slow speed movements, again with great control. Some fish use these other fins, either lateral, dorsal or ventral, to the exclusion of the caudal fins; examples of this include the rays and the knifefish.

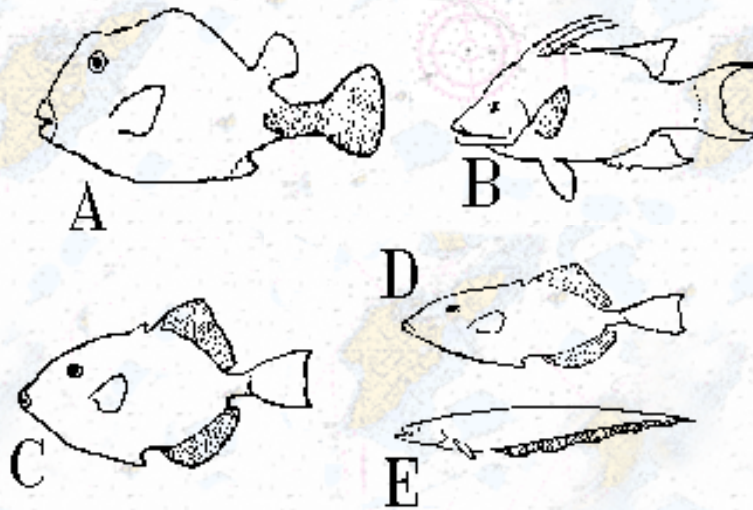


Figure 1. Above: Five fish showing body forms adapted for certain styles of swimming. A. Trunkfish showing ostraciiform swimming. Note the boxy body, the small peduncle, and relatively small tail. B. Wrasse showing labriform swimming. Labriform swimming is rowing using the fins; note the well-developed pectoral fins. Of course, the wrasse can move using the tail in a form of carangiform swimming. C. and D. Triggerfish illustrating balistiform swimming. Here the dorsal and anal fins move the fish with short-wavelength oscillations. E. Rajiform swimming as demonstrated by the knifefish. Movement occurs in response to long-wavelength undulations of the anal fin. Not illustrated: Carangiform swimming of many types shown by many fish, and anguilliform swimming as performed by eels, dogfish, lampreys, snakes, etc. Below: Images of a spotted eagle ray (left), a stingray (middle), and a flying grunard (bottom). The rays swim by rajiform movements of the modified pectoral fins. The flying grunard uses its pectoral fins as "wings" which allow it to leap from the water and glide for some distance.





Finally, one last form of locomotion should be mentioned (we'll still end up skipping a few). Snails and other gastropods often move by means of complex waves propagated across the interface between the foot and the substrate. The waves are caused by muscles, and, just like waves in the water, can cause motion. Crucial to this method of movement is the ability of the mucus secreted by the gastropod to bind tightly to the substrate at some points (pivot points), and flow freely at others, all as a result of changes in pressure.

## ***Resident Function Groups***

It is possible (and even useful) to group organisms according to how they move (or stay put) in the environment. In aquatic systems, for instance, we make distinctions between *nekton*, organisms which can swim, even against some currents, and *plankton*, organisms which, although they can move, are really at the mercy of the currents (plankton also tend to be microscopic). We also refer to *benthic* organisms, organisms that live on the bottom. There are many subdivisions of these groups. We have already discussed the various forms of swimming; let's move to some of the distinctions among benthic organisms (Fig. 2).

# Resident Function Groups

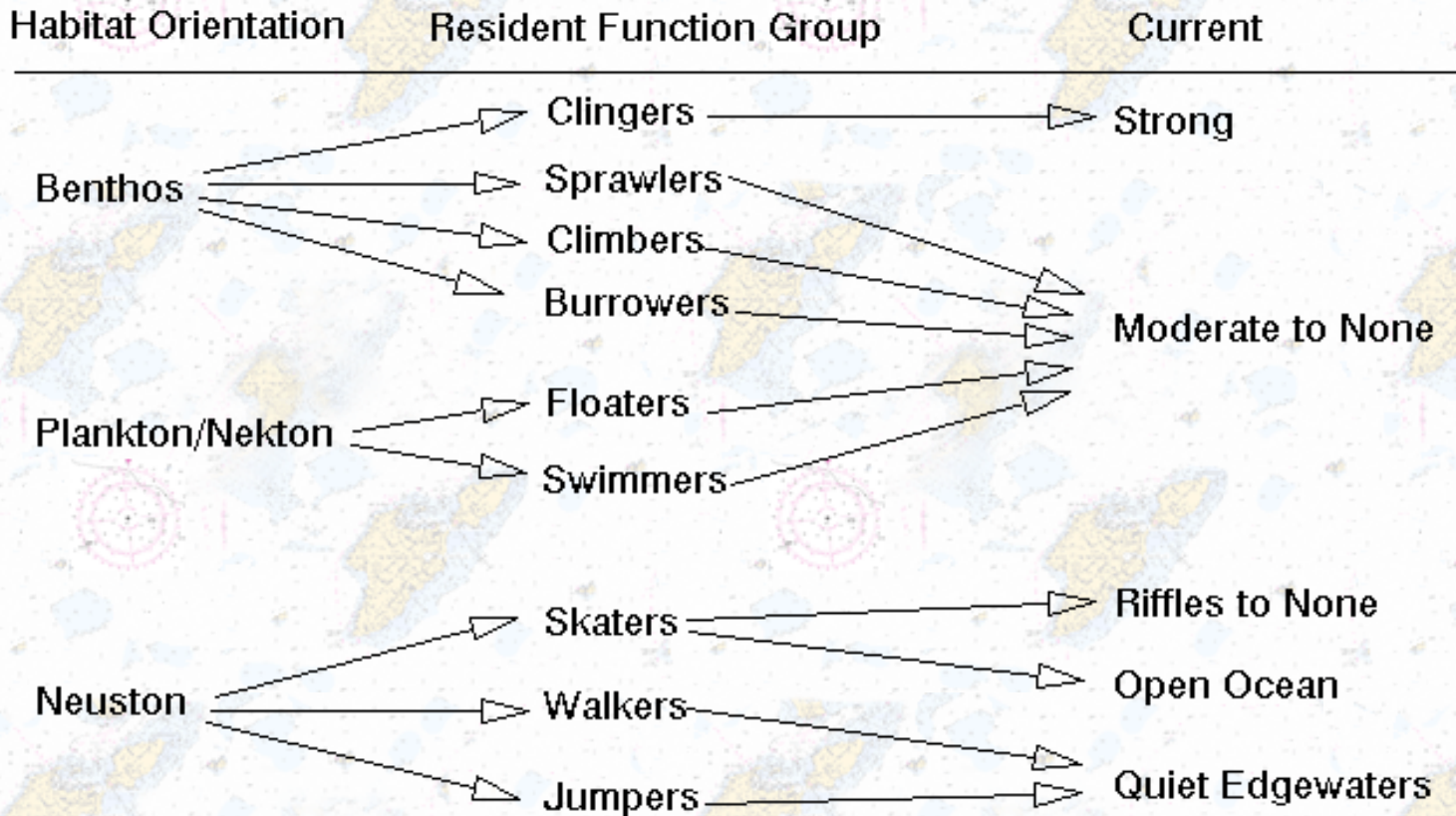


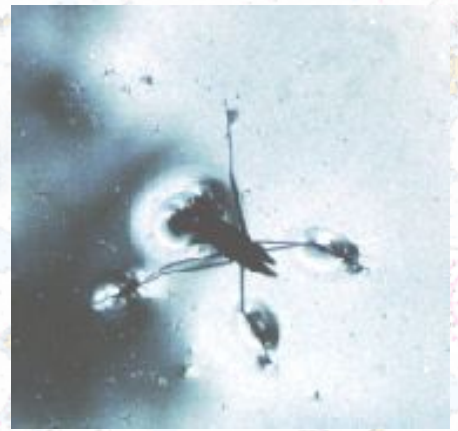
Figure 2. Resident function groups of aquatic organisms. The diagram shows the three main habitats for aquatic organisms, what resident groups are found in each, and what types of currents to expect in those habitats. As with many other classification schemes, these are only approximations and many exceptions occur in nature.

First, remember that benthic, as used here, includes not only the actual bottom, but any substrate in contact with the bottom, such as aquatic plants. Organisms that use claws or other means of attachment to hold onto the substrate are called *clingers*; if they hold onto plants we call them *climbers*. Both climbers and clingers are often distinguished by strong claws, and long legs; others have specialized means of attachment. For instance, *rheophilous* (current-loving) organisms like blackfly larvae can use silk to hold themselves in place; other organisms may have suction disks. In a sense, organisms like plants, which use roots to grip the substrate; and sessile animals such as crinoids or sea fans, which use root-like holdfasts to stay in place; are examples of clingers.

*Sprawlers* are organisms that live on the bottom (or in crevices within the substrate). They tend to be more mobile than clingers are, and lack specialized, permanent attachment structures. Many sprawlers are heavily ballasted with structures such as cases or shells that help them stay on the bottom.

*Burrowers* are organisms that live in the substrate. Some actively excavate the substrate to create a burrow; others simply move into crevices or burrows created by other organisms. If the organisms are so small that they can freely move between the naturally occurring pores in the substrate, they are termed *interstitial*. In many natural substrates, such as gravel or sand beds, the size of the interstitial pores are large enough that organisms such as tardigrades and rotifers predominate. These organisms are larger than most other truly microscopic forms and are often referred to as the *meiofauna*. Many burrowers line their burrows with silk or other materials to keep the burrow from collapsing. Burrows may be constructed to take advantage of natural currents to induce a water flow through the burrow for feeding or respiratory purposes; other organisms actively pump water through their burrows.

At the other end of the water column is the *neuston*, consisting of organisms that exist in association with the surface film. *Floaters* remain at least partially submerged, held at the surface due to buoyancy or attachment to the surface film (such as in mosquito larvae). *Skaters* glide over the surface of the water and include water striders (Fig. 3, right). *Walkers* move more slowly over the surface; some spiders can walk on the water's surface. *Jumpers* leap from the water surface; springtails and pygmy mole crickets are examples of jumpers.



As with any other classification system, there are problems with the above categories. Most organisms are capable of more than one of the above roles, at least at some part in their lives. Many aquatic organisms start out life as plankton, for instance, and as they grow, they are able to specialize. Others may change resident function group swiftly. For instance, how do you place a mayfly larva which crawls out from under a rock, scampers across its surface, drifts downstream with the current, then swims to another rock which it promptly burrows under?

## Further Reading

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# The Sensory World of Aquatic Organisms

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When we consider the senses, we typically think of the "five senses": hearing, seeing, tasting, touching, and smelling. Scientists usually look at the senses a bit differently, classifying them according to the medium which is being sensed. A physicist would speak of *chemoreception*, which involves sensing chemicals in the environment and includes both taste and smell; *mechanoreception*, which involves sensing mechanical deformation (movement) and includes touch and hearing as well as one's ability to sense movement, acceleration, stress on muscles, pain, and position of various parts of the body (proprioception); and, finally, *radioreception*, the ability to detect electromagnetic radiation, commonly known as sight. The ability to sense cold and heat would seem to be a type of radioreception, but we will consider it along with mechanoreception, since these receptors sense changes to the body rather than directly sensing conditions in the outside environment.

Our knowledge of the sensory structures and abilities of other species is better than one might expect, and the physiological and neurological basis of the sensory world of other organisms is also fairly well understood. Rather than simply reviewing what you should have learned, either in General Biology, Zoology, or Physiology, we will focus more on how sensory structures are applied underwater, with only brief introductory comments for each of the senses. You might want to review sensory structures in Keeton or in a Vertebrate Zoology textbook (Pough et al. 1989).

## Chemoreception

Chemoreception is divided into two main components, the distance sense, which we commonly refer to as smell or *olfaction*, and the contact sense, which we refer to as taste. In terrestrial organisms, the distinction is drawn out further, as olfaction detects chemicals in the air, while taste detects chemicals dissolved in water within the mouth. However fine the distinction becomes, there is a further one, at least in vertebrates. While the vertebrate sense of smell, perhaps most highly developed in some dogs, seems to be able to distinguish any of the millions of possible chemicals independently, the sense of taste merely averages responses of four generic chemoreceptor types (saltiness, sweetness, sourness, bitterness). Further, taste and smell are often processed together to give a combined sensation.

Olfactory senses overall are keen among some aquatic vertebrates; there is evidence that fish and turtles can distinguish the smell of the area (stream or beach) they were born in and use this information as a navigational tool. Invertebrates also have prodigious powers of olfaction, but these are best investigated for terrestrial species, and little has been done with aquatic species. For instance, we know of the ability of male moths to find female moths via pheromone concentrations so low it is likely that the male's initial contact is with a *single* molecule, yet we are not really sure to this day (1990) whether aquatic insects have any distance chemoreception at all. Such distance chemoreception is well documented in crustaceans, a group which evolved in water; it may be that insects, which evolved on land and then moved to freshwater, have not yet developed such a sense. In any event, the chemosensory abilities of those invertebrates which have been tested seem to indicate that invertebrates in general have heightened sensitivity to those particular chemicals (pheromones, chemicals given off by food, etc.) that are of primary importance, and lessened ability to sense chemicals of no historical relevance.

Most aquatic organisms have the olfactory cells mounted in a position where they will be exposed to moving water, presumably to limit time lags imposed by diffusion of the chemical through the boundary layer surrounding the sensory cell (remember that the boundary layer is smaller as water speed increases see Craig, 1990 page 352 *antennae*). For the same reason, perhaps, the olfactory organs are usually anterior on the organism, where the boundary layer is thinner, although many might argue that the anterior position simply allows the organism a better chance to smell what it's getting into. Vertebrates bear the olfactory cells in the nostrils, usually with arrangements for moving water over them; their taste cells are located on the tongue. Fish, the original aquatic vertebrates, have chemoreceptors scattered all over their bodies, but with particular attention to sensory structures such as the lips or barbels (Fig. 1). Invertebrates bear the olfactory structures on various parts of the body, often tentacles or antennae near the head, but also on mouthparts, feeding structures, legs, feet, tails, and so on.

Chemoreception in water is probably different than it is in the air. Chemicals move more slowly in water than in air. Also, the effect of currents cannot be overlooked (Fig. 2). Overall, in a stream or other aquatic system, chemical sensing is probably not as useful as it is in the air; for instance, pheromones seem to be rare in water, and use of smell to detect predators or prey is probably not as useful since organisms in still water can easily move faster than the chemicals they give off, and since in running water there is no sense of what is to the sides or downstream of the organism. Still, olfaction is useful at close distances and where light levels are low. The presence of chemosensory structures on the legs and feet of some aquatic arthropods suggest that these structures are really used more like mechanoreceptors to sense the chemical nature of the substrate (or whatever they have grabbed).

## Taste Receptors in a Catfish

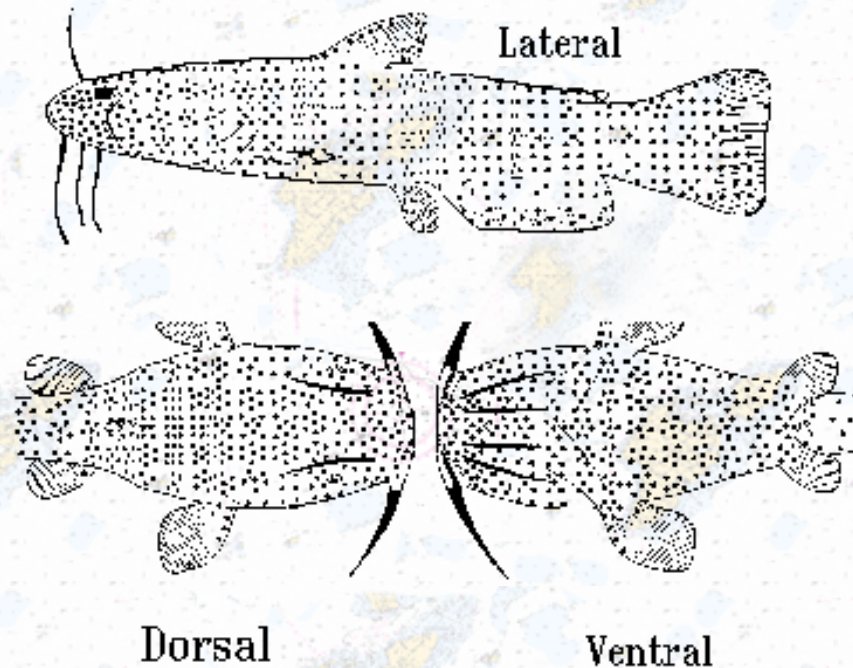


Figure 1. Location of taste receptors on a catfish. Each black spot indicates a set of chemosensory cells. Note that they are concentrated particularly on the barbels (whiskers) (From Pough et al. 1989).

The sense of taste in aquatic organisms is probably very similar to the sense of taste in terrestrial organisms. In both cases, the chemicals which will be tasted must be dissolved in water, and the only difference between the aquatic organisms and terrestrial organisms is that food comes wet to aquatic organisms.

# Effect of Current on Olfaction

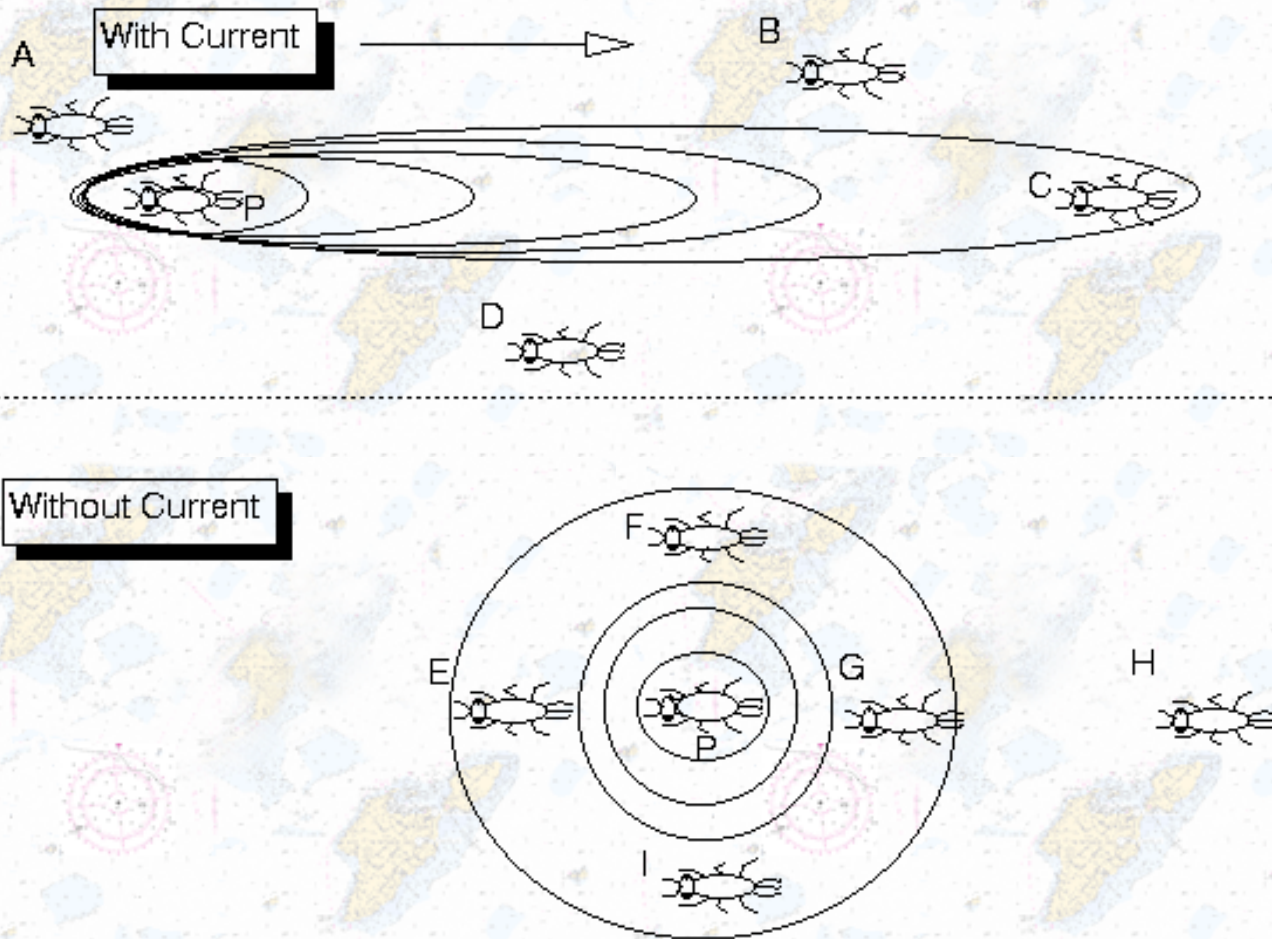


Figure 2. Olfaction with and without a current. In the upper drawing, the current forces the scent of the prey (P) into a long narrow plume. Organisms upstream (A) or to the side (B, D) cannot smell the prey, although organisms far downstream (C) can. Without a current, the scent diffuses in a circle, meaning that any close organism (E, F, G, I) can detect the prey, while an organism further away (H) cannot.

## Mechanoreception

The senses of mechanoreception are at least as well developed in aquatic organisms as in terrestrial ones. Among vertebrates, there are sensors in the skin that are sensitive to light and deep pressure, pain, heat, and cold. Other sensors gauge the strain on muscles, tendons, and ligaments and thus send information to the brain on the relative position of the various parts of the body in relation to each other. Organisms with exoskeletons are not as well endowed with such a range of sensors. The pressure sensors, for instance, would be of little use beneath a hard exoskeleton.

Most arthropods use *setae*, socketed hairs with nerve cells at the base, to detect contact with other structures, wind or water currents, etc. Special *setae* at joints are responsible for proprioception. *Setae* are often contained in structures with small crystals; these structures are known as *statocysts*; movement of the crystals as affected by gravity or acceleration in any direction is sensed by the *setae* and passed onto the brain. This gives organisms with *statocysts* a sense of gravity (which way is up?) and motion. A very similar, but more complex, system is used by vertebrates. Many vertebrates also use specialized hairs, such as those around the muzzle of a seal, to heighten the sense of touch.

The sense of hearing - distance mechanoreception - is used to detect movements in the fluid (air, water) surrounding the organism. This often gives information about what is happening some distance from the organism. The world, particularly the undersea world, is a noisy place, Jacques Cousteau's book *The Silent World* notwithstanding. Waves, undersea tectonic activity, swimming animals, vocalizations, rainfall, etc., all set up vibrations in the water that can be considered sound. Streams in particular are very noisy environments, with current sounds and rocks clicking together.

Some basic physics of sound: Sound travels faster in water than in the air; the exact speed varies with density and thus

with temperature, salinity, depth, and pressure. Adjacent layers of water with different densities can bend sound waves in unusual ways, creating effects where one organism might not hear another organism directly below it, while a third organism miles away at the right level might hear clearly. The U.S. Navy, which uses sound to locate enemy vessels (and depends on its own vessels not being heard), spends a lot of money studying how sound travels in the ocean, and knows more about it than anyone else - but they're not telling. Sound travels through a medium (despite what you hear on *Star Trek*, explosions in space are noiseless) and arrives as a series of pressure oscillations between high and low pressure. Humans can typically hear oscillations between about 30 oscillations per second (hertz) up to 20,000 hertz; dogs, of course can hear higher pitched sounds and thus their hearing extends past 20,000 hertz. Also, as a general rule, higher-pitched sounds are more directional, while it is hard to localize low-pitched sound. Placement of midrange and tweeter components, which carry the higher frequencies, in a stereo system is more critical than placement of the woofers, which carry only the bass (low-frequency) sound; bass does not contribute to the stereo image.

Certain organisms, such as whales and a few fish, use sound to communicate, but overall the practice does not seem to be as common in the water as it is on land where the air is full of the sounds of animals, particularly birds and insects, communicating. Perhaps this is the reason for Jacques Cousteau's title. But is there no communication taking place, or is it just so different that we don't recognize it? Two phenomena I will mention here suggest that the latter may indeed be the case.

One of the most fascinating experimental studies I have read (and you will too) was done recently by Barbara Peckarsky and R.S. Wilcox (Peckarsky and Wilcox 1989). Peckarsky has been studying predatory encounters between stoneflies (the predators) and mayflies (the predatees) in streams. She has been working for some time to document the ability of both predator and prey to sense each other chemically at a distance, an ability that her behavioral data indicates should exist. As a sidelight, she began to wonder if stoneflies could hear the mayflies as they swim away. She teamed up with Wilcox, who has a real mind for experimentation, and got some very interesting results.

First, they took living mayflies and glued tiny magnets to their backs. They got the mayflies to swim near a speaker placed in the water. The vibrations of the magnet as the mayflies swam induced tiny currents in the magnet of the speaker, and these currents were amplified and digitally recorded. The recordings were placed on microchips, much in the same way that music is sampled (you can buy a keyboard for about \$30 which can do this). They then placed dead mayflies or clear plastic models of mayflies with attached magnets in the water near living stoneflies and a speaker, and this time played back the amplified signal (the cone on the speaker was removed to prevent the actual sound waves from forming). The signal sent to the speaker caused it to produce magnetic waves which cause the magnets on the dead mayflies or models to vibrate the same way as the living mayfly had when it swam. The stoneflies paid a lot of attention to the models whenever the sound was on, indicating that they could 'hear' the swimming movements. Peckarsky called it a "hydrodynamic cue", but a vibration of about 2,000 hertz is well within what we normally call sound.

Similar abilities are well known to ichthyologists, long familiar with the *lateral line* of fish. The lateral line senses movement of the water around the fish. Much of this movement is what we typically would call sound (fish have a separate sense of hearing also). It is hard to imagine how the fish perceives that outside world through the lateral line, since we have no comparable sense. Still, we can observe fish in which the lateral line is damaged, and find that it is important for the fish to have an intact lateral line if it is to school with other fish, avoid predators, find prey, navigate between obstacles, and so on, particularly in turbid waters.

Other aquatic organisms which use distance mechanoreception include a wide variety of neuston which sense surface waves. For some, like water striders, this translates into an ability to find struggling (wave-making) organisms trapped in the surface film and thus home in on a potential meal; water striders also send their mating calls by vibrating the surface and making waves. Other organisms, such as the whirligig beetles (Gyrinidae), are even more sophisticated; they can use the waves they create as a type of sonar. Waves made by a gyrid bounce off objects in the water and return, and the beetle is able to use this information. How thousands of these beetles in an aggregation make sense of the many waves formed is still a bit of a mystery, however; presumably they use some kind of encoding system as do bats.

Use of sonar to tell how far away structures are is not confined to beetles, however. The skill is well-documented in many marine mammals, which produce sounds by making clicks with their tongues or other parts of the nasal-esophageal complex. These clicks are often at very high frequencies to improve both directionality and resolution, and may be further focussed by bodies of fat or oil in the head. It has been demonstrated that dolphins can resolve between objects very close in size; overall performance is probably better than what can be achieved with eyes in slightly turbid water. And, of course, sonar works equally well in turbid water or at night.

## Radioreception

Reception of electromagnetic information by organisms usually occur in that range of the spectrum having wavelengths between about 300 and 700 nanometers that we call light (Fig. 3). The shorter wavelengths in this range have the most energy and are known as ultraviolet or UV. Next comes the visual spectrum (for humans) or blues, violets, greens, yellows, oranges and reds. Finally, at longer wavelengths, is the infrared, or IR. Vision is restricted to these wavelengths for physical reasons. Shorter wavelengths carry too much energy and would damage the sensitive structures needed for

sight. Longer wavelengths often don't have enough energy, are difficult to focus, and when they are focussed require extraordinarily large eyes because of the long wavelength.

# Electromagnetic Spectrum

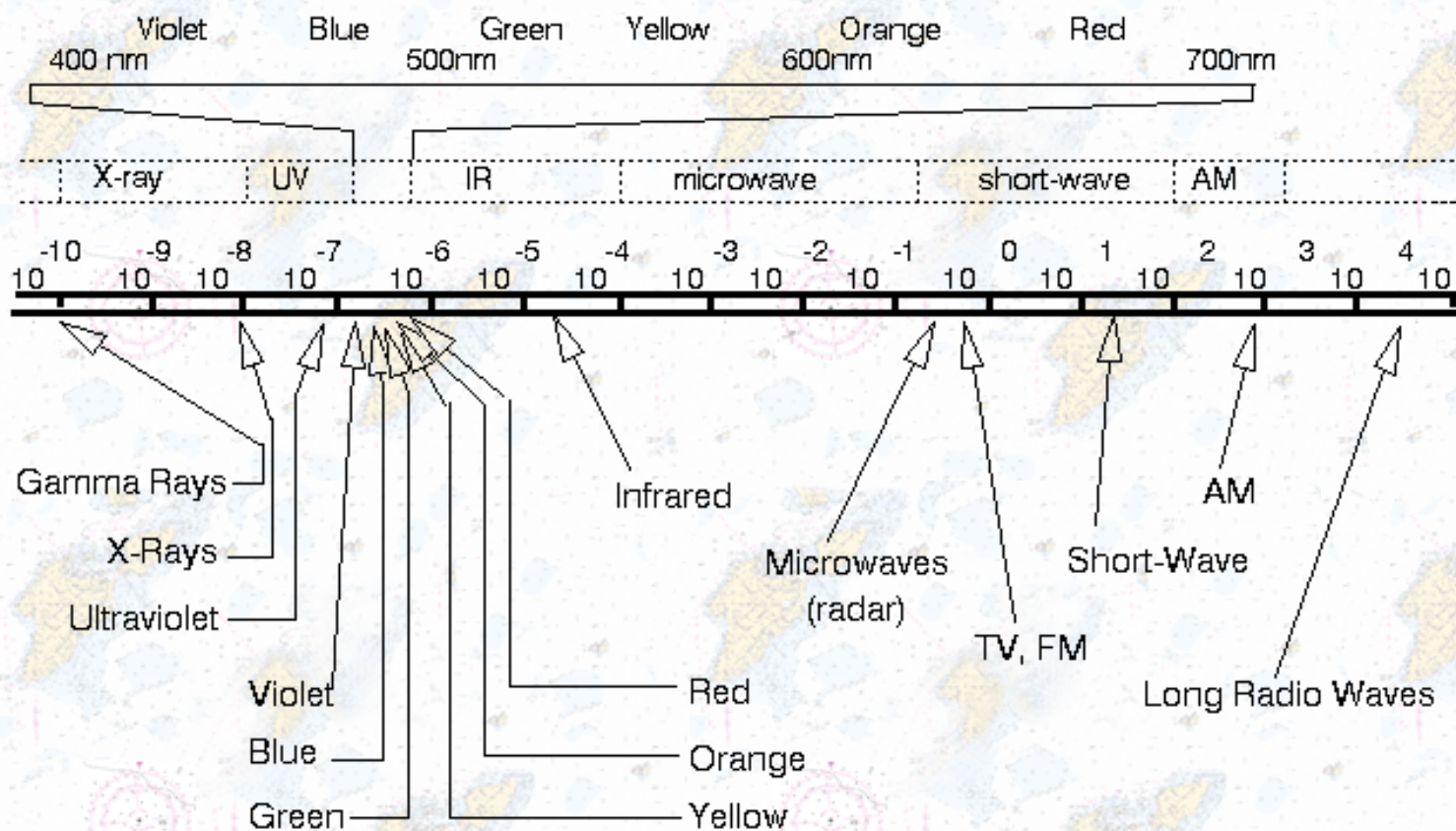


Figure 3. The electromagnetic spectrum. The region we call visual light (for humans, at least) is expanded in the upper figure. Wavelengths in the upper figure are in nanometers; in the lower they are in meters.

All light-related senses rely on photoconversion of chemicals by light in specialized nerve cells or photoreceptors. At the simplest level, photoreceptors simply indicate the presence or absence of light, and such a sense is all that many organisms need. More complicated photoreceptors can detect light intensity as well. The next step up is to form an image, and the biological world has taken two major paths. The *compound eye* used by invertebrates is composed of many separate components or *ommatidia*, each of which forms an image. Such an eye is very good at picking out movement; less good at picking out patterns. The *camera eye*, used by vertebrates and mollusks, is composed of a single optical unit with many individual neurons. Camera eyes form single images in the brain, and are better at picking up patterns than at detecting movement.

Color vision is possible in both systems. One simple method of obtaining color vision is to place pigments, which allow only selected wavelength to pass, in the light path of a neuron. When a neuron shadowed by a green pigment, for example, fires, the brain gets a message that green light has been detected. Vertebrate photoreceptors come in two basic types; rods, which are very light sensitive and form colorless, slightly fuzzy images in low light, and cones, which require more light and are individually sensitive to either red, green, or blue light. Cones form color images of great resolution. The ratio of rods to cones is high in nocturnal mammals (most mammals are color blind), and low in most birds (which have very acute vision).

Another important aspect of vision is the location of photoreceptors. Simple photoreceptors may be scattered all over the body, but more advanced systems are usually outgrowths of the brain itself. Often two eyes may overlap for at least part of their field-of-view, this allows for *binocular vision* and accurate depth perception, an advantage for predators or organisms moving in complex environments. Eyes which do not overlap to any great extent may allow the organism to

take in more at a glance, and are of particular use to prey species.

Water is not a good visual medium. As we saw earlier, light is attenuated in water, and turbidity exacerbates the problem. In many aquatic habitats, there really isn't enough light to see by our terrestrial standards. Organisms living in such water make extensive use of other senses, and are usually drab in color since color is meaningless. Colorful aquatic organisms usually signal the availability of light and clear water; it is no accident that colorful tropical fish come from clear waters, and that coral reefs, always located in shallow clear water, have an abundance of colorful species. Remember, though, that color perception changes with species and as the spectral composition of light changes with depth, so the "true color" of an organism can only be judged through the eyes of other inhabitants of its normal habitat.

Another problem that may occur with aquatic organisms which move between terrestrial and aquatic habitats is that of refraction. Simply put, refraction is bending of light that occurs whenever light moves from one medium to another - from water to air, or water to glass, for instance. Eyes which are adapted for the refraction that occurs at the interface of the solid, clear cornea and the air, for instance, will not be able to focus as well when the air is replaced by water. Organisms such as diving birds or turtles can compensate to some extent by having eyes with greater ability to focus, but this is only a partial solution. Humans solve the problem by using glass or clear plastic to encase a small volume of air over the corneas; this practice results in a distorted, but very clear image (the distortion manifests itself as magnification). Other organisms take another path. Both archerfish (camera eyes) and whirligig beetles (compound eyes) have developed additional eyes, so that they have one pair for use above water, and one below. The archerfish uses its terrestrial eyes to look for insects which it will knock into the water with a squirt of water, and its underwater eyes to watch for predators; the gyrenid uses all four eyes to scan for predators, which may come from above or below (they use their sonar to find food).

Because of the way light is attenuated in water, the ability to sense light above and below the human visual spectrum is not as common in water as it is on land. Insects in water probably can see some things in the UV spectrum, but apparently nothing like the IR vision of rattlesnakes has developed in H<sub>2</sub>O, where IR is absorbed quickly.

What water takes away in terms of radioreception of visual wavelengths is more than given back, however. Water is a much better conductor of electrical current than air is, and a number of organisms can detect electrical and magnetic forces. On the simple end, there are bacteria which can align themselves with the Earth's magnetic field; on the complex end there is the knifefish, which can discriminate between very small objects even in turbid water using its electric sense (Fig. 4).

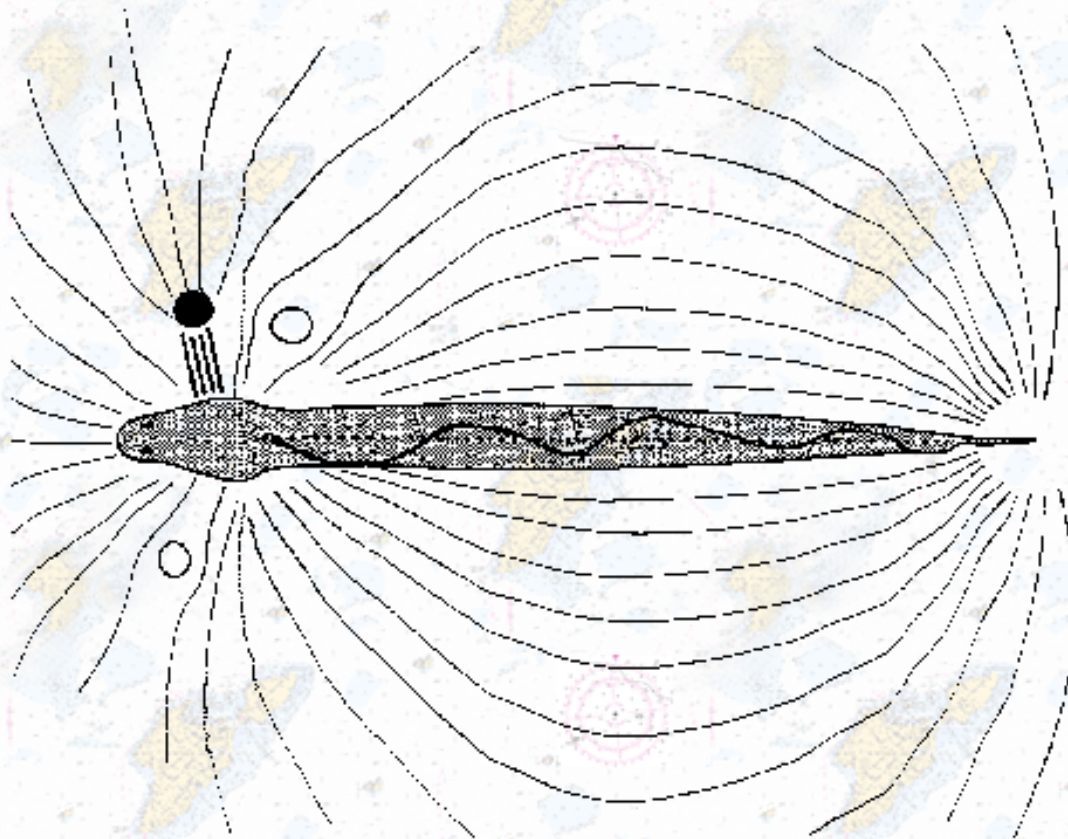


Figure 4. Electric sense in the knifefish. Electrical fields set up by the fish (lines) are affected by nearby objects (circles). Strong conductors such as living organisms (dark circle) cause the lines to converge, and this can be sensed by the fish. Weak conductors, such as inanimate objects (light circles), cause the lines to diverge (from Lissman, H.W. 1963).

All organisms produce electrical currents. A variety of aquatic organisms can detect these currents with specialized neurons. Such electrical sense has been found in a number of invertebrates and many aquatic vertebrates including sharks, fish, and even mammals such as the duckbill platypus. Electrical senses are important in turbid waters such as muddy rivers or the vicinity of a bleeding victim after a shark takes its first bite (scarlet billows, through the water ....). Often, the electrical sense neurons are concentrated near the head or in a structure that is placed in contact with a muddy bottom, such as the barbels on the chin of a catfish (which also have chemoreceptors), or the bill of a platypus. Other organisms go so far as to create their own weak electrical currents (modified muscles can do the trick) and actively search out prey. The latter is done by the knifefish, a denizen of muddy Amazon tributaries (Fig. 4). Active electrical senses work best when the body is straight, so the knifefish has abandoned normal propulsion via the tail in favor of propulsion via undulations of the dorsal and ventral fins. Still other electrical fish, such as the electric eel, catfish, and ray, take the generation of the electrical current a step further; they typically generate enough electrical current to stun their prey or dissuade a potential predator.

Further Reading:

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## Feeding in Aquatic Organisms

We have considered many aspects of living in water, from the physical and chemical basics to the topics of osmoregulation, respiration, locomotion and sensory perception. We have discussed how plants obtain the dissolved gasses and inorganic nutrients that they need for photosynthesis; now it is time to consider how animals obtain the chemicals they need for life.

There are two basic sources of food for aquatic organisms. Photosynthesis uses energy from the sun to incorporate CO<sub>2</sub> into carbohydrates, which animals can break down for energy; chemosynthesis uses the energy inherent in reduced metal compounds for the same purpose. Photosynthesis in water is a surface phenomenon; organisms in the deep cannot use photosynthesis directly. Chemosynthesis usually requires an anoxic environment, and in the modern world is limited to certain small, scattered habitats.

Plants can be divided into the algae, which are small, easy to ingest, relatively diffuse in the environment, and relatively hard to digest. Higher plants are large, hard to ingest, and hard to digest, and in any event, are relatively rare in aquatic habitats. Plants in general are a food of intermediate quality. Animals are mobile, they may fight back, and therefore are overall usually hard to ingest, but once ingested they provide high-quality food that is easy to digest. *Detritus*, which consists of decaying plants, animals, and animal waste, comes in a variety of sizes, is usually easy to ingest, is usually easy to digest, but is also of the lowest quality.

To summarize, animal material is of the highest quality, is the easiest to digest, but is the toughest to ingest. Plants are of medium quality, are easy to get, but may be tough to ingest, and are almost always tough to digest. Detritus is the easiest to ingest, is of medium digestibility, but has the lowest quality. Of course, these are generalizations; for instance, a recently killed animal is technically detritus but is of far above average quality. The food source for an organism can be very important in its life cycle. For instance, mosquito larvae, which feed on low-quality detritus, often reach the adult stage without enough protein to produce eggs, thus forcing the females to seek out blood meals. Organisms that feed on decaying wood (mostly cellulose) often depend on symbionts or fungi to obtain protein. Plant feeders must overcome not only thick, indigestible cell walls, but also a host of chemical toxins stored by the plants to dissuade herbivores.

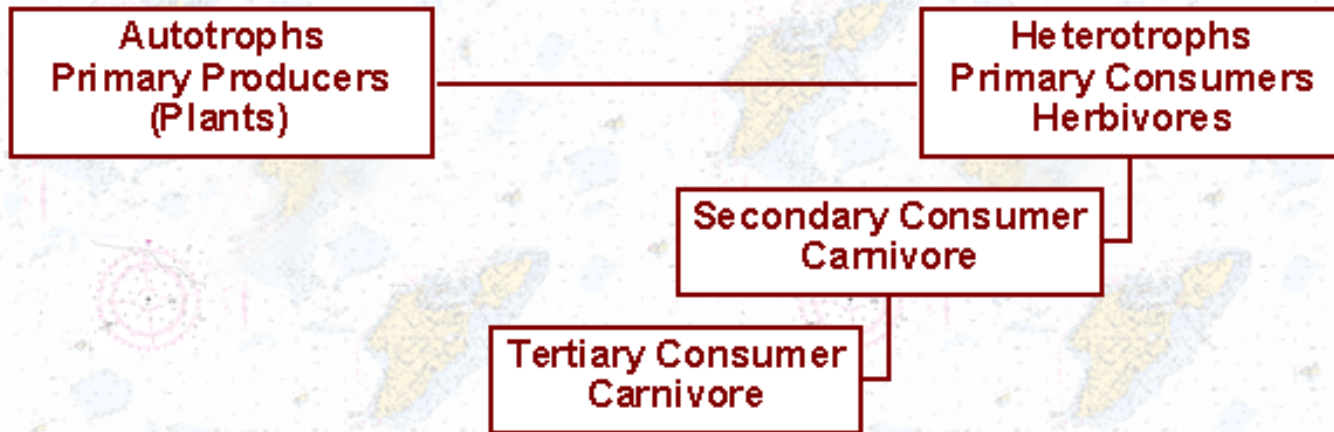
There are several ways to divide the continuum that animal feeding modes fall into up into discrete categories, and, after 10 years of research into how aquatic insects feed, I can tell you that about the only generalization that you can make about animal feeding habits is that most animals are opportunistic - they will eat whatever is available. There are specialists, and there are organisms that specialize some of the time, but a lot of animals simply resist being classified as to feeding type, particularly if you observe them over their entire life cycle. This tendency seems to be especially true for many aquatic organisms, which tend to be generalists. Indeed, it might be argued that a high degree of specialization in feeding is largely a phenomenon confined to terrestrial organisms and parasites.

With that in mind, we will nevertheless attempt to categorize feeding in aquatic organisms. The next hurdle comes in trying to decide how to make the distinctions between feeding groups, that is, what criteria to use. There are several different criteria that can be used, and each reveals a different type of information. The choice of which system to use is thus largely a function of the type of information you wish to gather.

### Dietary Feeding Groups

Often ecologists are interested in tracing the flow of energy through an ecosystem. From this standpoint, a system that keeps track of diet is valuable, particularly if that diet is related to what are known as *trophic levels* - where in the food chain the energy present in the prey came from. Such a system typically divides the world up as follows:

# Feeding Groups



This system could be continued on through 4<sup>o</sup> and 5<sup>o</sup> consumers and so on until the end of the food chain is reached. Another, similar system is also included above and includes the old favorites *herbivores* and *carnivores*. The advantage of this system is that you can make predictions of population size and energy flow if all the organisms stay in their groupings. For instance, a general rule of thumb for food chains is that only about 10% of the energy at one level is available to be transferred to the next. So, if all your organisms have about the same *biomass*, you would expect to have about 10x as many plants as primary consumers, 10x as many primary consumers as secondary consumers, and so on.

The big problem with this type of system is that organisms do not always fall into such neat categories. Some animals are *omnivorous*, eating both plants and animals; some animals are *detritivores*, feeding on decaying plant and animal remains or wastes, often without regard to the origin of the material, and it is unrealistic to expect a hawk to think "gee, I've been classified as a tertiary consumer, so I better eat only secondary consumers, and that means asking this snake to be sure she's only been eating primary consumers, so that when I eat her I don't inadvertently become a 4<sup>o</sup> consumer ...". In other words, animals ignore the boundaries and the ecologist must determine what percent of the animal's nutrition comes from each of the other trophic levels. This makes things a great deal more complicated.

There are other diet-based classifications as well; some of which work pretty well for specialists that concentrate on a particular type of food. For instance, we can speak of *piscivores* (fish eaters), *insectivorous* plants, *frugivores* (fruit eaters), or even *coprovores* (dung eaters).

## Functional Feeding Groups

An alternative to a diet-based classification is one based on how the food is ingested. These systems are sometimes known as *functional feeding groups* or FFG's. These FFG's arise almost ad hoc as workers describe feeding modes for organisms they are studying, without regards for what workers dealing with other groups of animals are doing. FFG's are based on physical characteristics of the food. I would suggest the following four continua as the characteristics by which food can be classified:

1. Size - micro to macro (relative to organism feeding)
2. Degree of attachment - suspended to deposited to attached
3. Origin - protist to plant to animal
4. Condition - living to dying to decomposing

Note that the diet-based classification scheme is based on the last two continua, origin and condition. FFG's are usually based more on the first two, size and degree of attachment.

One fairly good system for aquatic insects was developed originally by Merritt and Cummins (1978). It was greatly improved by a paper that came out a decade later (McShaffrey and McCafferty, 1988). Before we get into the details, though, a little background is needed.

There are several sources of food for aquatic insects. These sources include algae, both attached (*periphyton*) or as plankton, other insects, fish, vascular plants, and detritus. This food can be further divided as to size, either microscopic or macroscopic, and degree of attachment to the substrate, from suspended in the water (*seston*) to loosely deposited on the substrate to actually attached. Traditionally, the feeding categories in Merritt and Cummins were assigned after

looking at the gut contents of the organisms in question. This is a risky business because gut contents are hard to identify and, since the organisms are so opportunistic, gut contents may vary from day to day (or season).

A much better way to determine what an animal is eating is to actually watch what the animal eats, a common-sense approach rarely employed in the past. To be fair, it is extremely difficult to observe feeding under natural conditions; these are, after all, small organisms, living underwater, often in flowing, turbid waters, often in the dark under rocks. Furthermore, accurate determination of the function of different feeding structures is impossible without detailed movement analyses and magnifications of the feeding structures above that possible with a light microscope. Scanning electron microscopy solved the second problem, and inexpensive consumer video equipment, which began to appear in the 1980's, solved the first.

By combining these tools, I was able to observe feeding in detail, and correlate feeding structures and feeding habits. With this data now available, it is possible for me to make fairly accurate predictions as to what an organism eats and where it lives simply by examining its structure (people at scientific meetings often bring me pictures and ask me "what does this thing eat?"). The feeding scheme I devised along with Dr. W.P. McCafferty modifies the Merritt and Cummins scheme by including this new data and providing *functional* (as opposed to dietary) definitions for some of the groups defined by Merritt and Cummins. The McShaffrey-McCafferty scheme works for *microvores* (those which feed on microscopic particles) among the aquatic insects (and also among many other benthic aquatic organisms) and is stated as follows (from McShaffrey and McCafferty, 1988):

- ○ "The ability of an organism to use more than one mode of feeding, whether it be *R. pellucida* scraping and brushing, or *S. interpunctatum* using the same mouthparts to brush, collect-gather, or filter; or different developmental stages of a single species using different feeding methods (Cummins 1973, Cummins and Merritt 1984), complicates the problem of pigeonholing species into FFG's. This complexity is aggravated by attempting to assign FFG's based on gut contents that are often unidentifiable. Our study of *R. pellucida* and other aquatic insects suggests that a more mechanical approach to delineating FFG's for benthic insects that feed on relatively small materials (microvores, sensu McCafferty 1981) may be appropriate. In this scheme, potential food material, regardless of origin, is viewed in terms of a continuum ranging from material suspended in the water, to material settled on the substrate, to material bound or growing attached to the substrate. Various feeding strategies are adapted to deal with various sections of this continuum.

In our scheme, benthic microvores can be divided into two basic groups, Filterers and Collectors. Filterers derive food material from the water, and the filter may consist of either parts of the body or manufactured devices such as silk nets. Passive filterers rely on seston already moving to their filtering apparatus, whereas active filterers generally resuspend deposits to filter. Thus, depending on the immediate source of the food material, we classify benthic filterers as either seston filterers, or deposit filterers. Collectors remove deposits or attached material from a substrate by direct contact of the feeding structures with the food material. Collectors can be divided into three groups: brushers, gatherers, and scrapers. Brushers use setae to obtain loose or lightly attached material and are often morphologically, functionally and behaviorally close to deposit filterers. Gatherers feed on similar materials but primarily use structures other than setae for food gathering. Scrapers have adaptations that allow them to feed on tightly accreted material.

To summarize, benthic filterers and collectors exhibit a range of feeding strategies for feeding on a spectrum of small particles ranging from suspended materials (seston filterers) to deposits of various integrity (deposit filterers, brushers, gatherers) to firmly attached materials (scrapers). As is the case for *R. pellucida* and *S. interpunctatum*, species may not be limited to one strategy. This scheme is attractive because habitats can be characterized hydraulically, and the FFG composition of the microvore community can be estimated based on the physical state in which the hydraulic forces will place the food material. In this context, concepts of community development can be based on the relative amounts of microhabitat available to provide food material in different positions in the environment and with different propensities for attachment. One drawback of such a classification system is that it provides little information about the origin of the material (i.e. primary production, detritus, etc.); however, under natural conditions many benthic macroinvertebrate microvores feed on a variety of materials and only a relative few species are dependent on a single trophic level for their food resources. As indicated above, the system excludes macrovores such as shredders, miners, engulfers, and many predators.

It remains premature to erect a new FFG classification system; however, such a system may become necessary as the behavior of more species of aquatic insects is studied in detail. For instance, Dahl et al. (1988) recently presented a classification scheme of FFG's for the Culicidae that also further divided the FFG's of Cummins and Klug (1979) into more discreet groupings based on the mechanism of food acquisition. It is notable that Dahl et al. (1988) chose to use the term brushers to describe a feeding system found in certain Culicidae. Those authors were evidently unaware of the brusher concept of McShaffrey and McCafferty (1986); from their discussion it is not clear whether their mosquito "brushers" feed by direct contact of the mouthparts with deposits (as is the case with *S. interpunctatum*), or if the mouthparts create a current which carries the material to the mouthparts (deposit filtering, herein), or both. "

With this feeding classification, which uses only the first two of our food classification continua (size and degree of

attachment), there is little information on where the material originates, which is O.K., because the food in actuality originates in many places. For instance, a collector will be feeding on detritus, settled plankton, and animals simultaneously, defying classification in any one diet-based category. Because the FFG's are tied to the morphology of the animal, it is less likely (but still probable) that the animal will "break type", that is, a filter feeder spends most of its time filtering.

The McShaffrey-McCafferty scheme is probably too detailed for our use. As far as discussions of feeding go, we will use whatever scheme is appropriate. We will often talk in terms of dietary classifications, but for those times when a functional classification is more important, perhaps the scheme below will work:

### Microvores

- Suspension feeder (suspended material)
- Deposit feeder (unspecialized, loose, settled material)
- Grazer (attached material)

### Macrovores

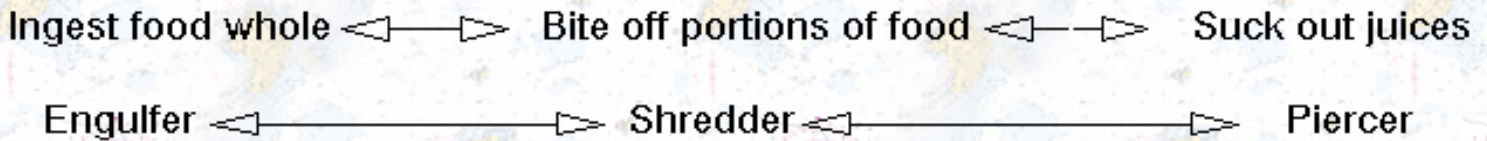
- Shredders
- Engulfers
- Piercers

Let us explore each of these groups in a little more detail (see also Fig. 1). **Suspension feeders** are the filterers of the McShaffrey-McCafferty scheme. They filter small particles from the water using a variety of techniques. Before we look at some examples, we must correct one bias that we have about filtering. Our concept, rooted in our high Re world is more of sieving than filtering. We see a filter as some sort of sieve, and the things retained by the sieve are those too big to fit through the holes. At low Re, that is only one possible mechanism. Smaller particles that you would expect to go through the filter may become entrapped due to gravitational forces (between the particle and the filter), electrostatic charges, or through what is known as inertial impaction, among others (Rubenstein and Koehl, 1977). What this means is that at low Re you can't judge what size particles will be filtered out simply by examining the mesh size - the size of the holes.

# Functional Feeding Groups

## Macrovores

### Food Ingestion



## Microvores

### Condition of Food

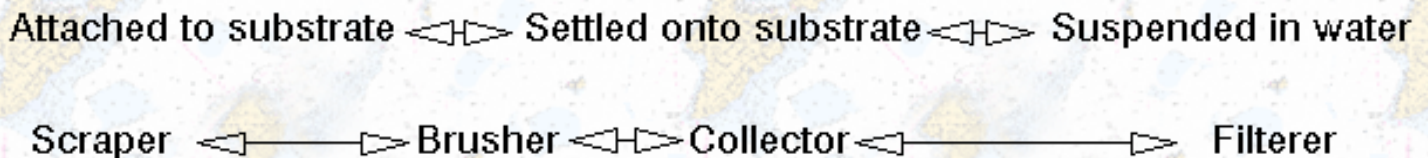


Figure 1. Functional Feeding Groups, shown here as functions of food size (macrovores) or degree of attachment of food to the substrate (microvores). Among the macrovores, the continuum encompasses the size of the prey as it is ingested, ranging from simply swallowing the prey whole (engulfer), to biting off pieces of the prey (shredder), to only ingesting the juices of the prey (piercer). Among the microvores, the continuum is drawn over degree of attachment of the food to the substrate, and ranges from tightly attached, to deposited, to suspended. In this scheme, scrapers remove tightly bound material; brushes remove more loosely bound material and cross over to material that has simply settled out; collectors remove deposited material; and filterers remove material from the water column.

As we have seen, filter feeders can be active, creating their own currents, or passive, letting water currents do the work. Let's examine some of the filtering structures used by animals. Sponges utilize the flagella of the collar cells to create a current; food settles out at the collar cell. Tunicates use water currents often generated by cilia to bring food to the pharynx, which is highly perforated to allow the water to pass, while the food is retained on a mucus coating. A similar scheme is used by bivalve mollusks such as clams. Lophophorates use mucus-covered tentacles in conjunction with ciliary currents to trap food; tunicates use the perforated pharynx as a filtering basket and in some species use the exhalant filtering current for propulsion. Some species use nets of mucus. Tentacles are also used by some filter-feeding echinoderms such as crinoids. Arthropods use either setae (hairs) for filtration, or they weave silk nets to filter material from the water. Many arthropods place the filtering structures on legs or other appendages where they can actively be moved through the water; such is the case for most of the planktonic crustaceans. Often the difference between a filter and a paddle is very slight, minute changes in the spacing of the setae or the speed of travel may make a huge difference (Rubenstein and Koehl (1977)). Some filter feeders such as crinoids are little removed from deposit feeding cousins; their short stalk simply gets them above the substrate and gives them "first shot" at settling material. Remember that filter feeders include the largest organism that ever lived - the blue whale, which feeds by swallowing a huge mouthful of water and then spitting it out through highly modified teeth known as *baleen*. You can simulate the effect by taking a spoonful of cereal or soup and spitting it out through your teeth. Do this in front of young children and tell their parents you are teaching them about nature. The parents will love you.

**Deposit feeders** would be the gatherers and some of the brushers of the McShaffrey and McCafferty scheme. Some of them even cross the line a bit into filterers because they move to a deposit and stir it up and then filter out the food. Deposit feeders are generally feeding on detritus, dead and decaying animal or plant material that has fallen to the bottom. *Coprophagy* (eating feces) is also common among deposit feeders; some food items may end up passing

through the guts of several animals. Since the material is loose and unattached, little specialization is needed in feeding structures. Any way to shove the food into the mouth will usually work; this even includes burrowing through the deposit with your mouth open. Many aquatic crustaceans use structures that resemble the filtering structures found on true filterers, and other organisms use mucus strands or nets in conjunction with cilia. At the other extreme, for material that is somewhat more cohesive, variations on the scraping strategies below will be employed. Brushers, for instance, are really a cross between a filter-feeder and a scraper.

Removing tightly bound material such as some diatoms or attached algae is a lot of work. **Grazers** can exploit this relatively (compared to detritus) high quality food where most deposit feeders cannot. Perhaps the most successful scraping structure in the animal kingdom is the *radula* of mollusks such as snails. Basically a series of small teeth that can be dragged over the surface to dislodge food, the radula is what separates the mollusks from the flatworms and is in large part responsible for the enormous success of the mollusks. Aquatic insects may duplicate the mechanical properties of the radula with specialized chitinous setae on their mouthparts, or with their claws. A researcher at Bowling Green and I are looking into the uncanny resemblance of snail and insect scraping structures. Other grazers might include fish such as the parrotfish which bites off pieces of coral and digests the polyps and associated organisms and expels the sand (much of the coral sand of the world starts out as parrotfish feces; think about that the next time you spread a towel). You should also be aware of the tendency of terrestrial ecologists to use the word grazer to refer to animals that feed by cropping grass and other short plants.

Organisms that feed on large pieces of food, macrovores, can be divided into three main groups depending on how they ingest the food. If they bite it off they are **shredders**; if they swallow it whole, they are **engulfers**; if they suck it out, they are **piercers**. Most vertebrates except lampreys and vampires are either engulfers or shredders. Engulfers and shredders will usually have teeth and jaws (or their equivalent) to facilitate feeding. Teeth may be sharp to hold prey before it is swallowed whole, or may be modified to cut or crush the prey. Herbivores in particular often have crushing mouthparts to break up tough cell walls and extract the contents; carnivores often have tearing or holding teeth. The beak of turtles, birds, cephalopods, and some fish is another tearing structure. Carnivore engulfers and shredders may employ specialized strategies and structures to capture prey (gory details later).

Macrovore piercers use a different strategy. They pierce the surface of their food and suck out its juices, often with the help of digestive enzymes. This is a common feeding method terrestrially, as anyone bothered by mosquitoes can attest. In aquatic systems it is also practiced by insects such as giant water bugs, by lampreys, and even by some mollusks such as clam larvae which are ectoparasitic on fish. Some aquatic insects even suck the juices out of plants in this way.

Another type of feeding which technically is a type of macrovore feeding is parasitism. In aquatic systems this will include *miners*; organisms (usually insects) which chew their way through the insides of plants sort of internal shredders). Animal parasites usually chew their way through the host tissue or simply absorb nutrients.

### Evolution of Feeding Strategies

At this point, let's stop and consider how various feeding strategies may have evolved. The first multicellular animals (Fig. 2) probably ate each other, bacteria (including cyanobacteria), and protists. This diet seems limited until you consider that at the time of the first multicellular animals, that was all there was to eat. The descendants of these organisms that are still alive today are filter feeders (Porifera), carnivores (Cnidaria, Ctenophora), or deposit feeders (Placozoa, Mesozoa, and Platyhelminthes). The real story in terms of evolution of feeding strategies begins with the flatworms.



aquatic systems, of course, most of the plant material ingested is either phytoplankton or algae scraped from rocks.

Among detritivores, the trend seems to be an effort to get the freshest detritus (and a mix of small living organisms if possible). In aquatic systems this means intercepting the material before it gets to the bottom. This factor encourages the development of stalked forms such as crinoids, lophophorates and brachiopods; large filtering structures such as poriferan colonies; and mobile filtering such as in whales, some tunicates, and others.

The development of terrestrial vascular vegetation also encouraged the development of successful strategies for ingesting such plants, and where vascular plants have reentered the water, terrestrial herbivores have soon followed. Examples of these would include a host of aquatic insects and even such large mammals as the manatee.

## The Gut as it Relates to Feeding

The gut of most organisms can be divided into three functional regions - the *foregut*, the *midgut*, and the *hindgut*. Some organisms, however, do not have a through gut and thus will not have these regions; flatworms, Cnidaria, sponges and many parasites for instance do not have through guts of this sort.

In organisms with through guts, the divisions are both spatial and functional. The foregut usually consists of a *mouth* adapted for ingesting food. Often the mouth plays a very important role; the flexible cheeks of many fish and turtles help suck in prey. The mouth cavity may be the site of initial digestion if salivary glands are present. Chewing and tearing structures in the mouth may also begin physical digestion of the food. Posterior to the mouth is the *pharynx*, which in some organisms simply begins the process of swallowing; in others the pharynx forms a pump for sucking fluids into the mouth. Some fish such as the carp have pharyngeal teeth that also process the food as it is swallowed. Behind the pharynx is the *esophagus* used to connect the mouth with the *crop*, a food-storage organ. Organisms that feed only infrequently, such as several deep-sea predatory fishes, may have crops that can enlarge to a size greater than that of the entire body before eating.

The midgut begins with the *stomach* (often combined with the crop). The stomach's role is to initiate chemical digestion through the addition of secretions containing digestive enzymes from various digestive glands. The muscular stomach also continues physical digestion by churning the food along with the digestive juices. Some stomachs have teeth or grinding structures to further break up the food; stomachs of this sort are often called *gizzards*. Many organisms have various blind sacs or diverticula leading off the main digestive tract just posterior to the stomach; these structures provide more room for digestion and more surface area for absorption. Such structures are more common in herbivores. The *intestine* follows the stomach and is the site of nutrient absorption. It often is highly coiled, or has many internal folds, both ploys to increase surface area. As a general rule, the intestine of an herbivore will be longer and more coiled than that of a carnivore, since it takes more time (space) to remove nutrients from plants than animals, and because more plant material must be processed to obtain the same amount of nutrition.

The hindgut is the site of feces storage and water reclamation. The later process is, of course, more important to terrestrial organisms than aquatic ones, but remember that even in some aquatic organisms such as aquatic insects, chloride cells in the rectum are an important factor in osmoregulation.

The presence of cellulose and certain other molecules in food provides a definite challenge to digestive systems in animals. As mentioned before, few animals have developed any cellulase at all, and what is present is not very effective. Other molecules may be encountered too rarely to exert enough selective pressure for the development of specialized digestive enzymes for those molecules. The answers in both cases are *symbionts*, bacteria and protists that break down complex molecules in the gut and often make up bulk of feces. These symbionts often live in the diverticula of the digestive system, and, of course are more important to herbivores. They are widespread in aquatic organisms. Problems with symbionts include both initial inoculation of the gut and maintenance of a significant population in the forward reaches of the gut (since the movement in the gut is all "downstream"). The former (and often the latter) is often taken care of by coprophagy (eating dung); even in animals feeding on plants or attached algae some feces may be ingested. Mammal young probably pick up their inoculations from their mother or nestmates. If food tends to pass through the gut too fast for digestion or the maintenance of symbiont populations then *autocoprophagy* may result, where the organism eats its own feces.

## Predation - Some More Details

The phenomenon of predation places some common selective pressure on organisms that feed in this way. Although there are many different ways to capture and/or feed on other organisms, the basic problems remain similar, and it is no surprise that similar solutions have evolved among carnivorous animals regardless of taxa. In order to feed on other organisms, they must be found, caught, killed, and ingested.

Finding prey often involves sophisticated sensory structures. All senses are used by predators in detecting potential prey. We are perhaps most familiar with sight, which, as it turns out, is perhaps the least used in water, since water is often dark and/or turbid. Still, there are a number of predators that use sight to some extent. These are primarily organisms that

feed in shallow, clear habitats such as coral reefs, although our best local representatives might be centrarchids such as bass and bluegills. On land, predators are often told from herbivores by the presence of forward-directed eyes with good overlap of the visual field for stereoscopic vision, a necessity in gauging distance to the prey. Herbivores usually have lateral eyes with wide peripheral vision. In aquatic systems, however, this system breaks down, with only the top predators, such as alligators, having much in the way of stereoscopic vision. Other predators, such as bass, are simply too vulnerable to predation themselves, particularly when young.

Sound and related disturbances in the water are frequently used by predators to find prey. We are of course familiar with hearing as a tool in locating prey, but of course fish also have the lateral line to help them sense disturbance in the surrounding water. Marine mammals often use sound waves that they themselves generate to locate prey by bouncing the sound waves off the prey. This sonar is a highly advanced sense, and porpoises at least are able to discriminate between objects very close in size with their sonar. Their sonar sense, in fact, may have better resolution than vision under all but the clearest conditions. The sound waves that are generated have a short wavelength and are above the normal hearing range for humans. Many marine mammals have a "lens" of fat or oil in their head that serves to focus the sound waves, making this sense highly directional as well. The use of sound to locate prey is not limited to vertebrates, either. Recent evidence (Peckarsky and Wilcox, 1989) indicates that stoneflies can "hear" the swimming movements of their mayfly prey.

Perhaps the best distance sense in water is olfaction. Many predators can home in on their prey by scent alone, and, of course, many prey learn to avoid areas where the scent of potential predators is strong. Olfactory senses are strong among most aquatic organisms with the possible exception of aquatic insects, which perhaps have not developed these senses to their fullest potential yet. Apparently, the great feats of homing attributed to salmon, eels, and sea turtles in returning to the river (or beach) of their birth to mate and reproduce is due in part to an ability to chemically distinguish between different sites. Sharks have been known to follow blood trails of their prey for miles, and crayfish in tests have responded to vanishingly small dilutions of extracts from their food sources. Of course, as a distance sense, olfaction in water is at the mercy of the currents; for instance, in a stream a predator cannot detect the scent of a prey organism just slightly downstream, while it may be able to detect other prey far upstream. Similarly, turbulence in the water may either confine the scent to a narrow, concentrated stream or spread it into a wide, diffuse band. The former makes it easy to home in on the prey once the stream is detected, but the chance of detecting the odor is slight; in the latter, it is easy to detect the scent, but hard to home in on it to find the prey.

Other senses are commonly used in water as well. Perhaps the most important of these is the *electric sense*, the ability of specialized cells to detect the weak electrical energy given off by all living things. Because water conducts electricity, this sense is particularly well developed among aquatic organisms, especially those living in murky water. The ability to exploit electrical senses is found in both vertebrates and invertebrates, but is best studied in the vertebrates, where it is found in all major groups. The duck-billed platypus, for instance, uses electrical sensors in its bill to locate food in the mud. Sharks use the electrical sense to make the final biting lunge for their prey; at close range the smell of the prey is overpowering, and the eyes may close (or the water becomes cloudy with blood), making vision difficult. Other organisms, such as the knifefish, take the electrical sense further, generating their own stronger electrical currents and using these to "probe" their surroundings. The electrical current is generated by modified muscle cells, and for the system to work properly, depends on the body being kept in a straight line, thus forming the selective pressure for the unusual form of swimming exhibited by the knifefish, which uses its anal fin for propulsion, eliminating the need to bend the spine. Still other electric fish go further still; after locating prey with the electric sense they generate a powerful current to stun or kill the prey; you are no doubt familiar with electric catfish, eels, and rays.

At very close range, the sense of touch may be very important. This is particularly true of invertebrates, although it is of course used by vertebrates as well. Some damselfly larvae, for instance, locate their prey visually and use strong stereoscopic vision to maneuver into the proper position. The final lunge in some species, however, is controlled by the antennae, which are used as range finders. When the prey is in contact with both antennae, the range and position are ideal, and the antennae spring back out of the way, allowing the labium to spring forward and capture the prey (Fig. 3). Stonefly larvae also play their antennae over their prey before lunging. Apparently they get both directional and other information from this. An anti-predatory device employed by some mayflies seems to work to fool stoneflies; when touched by the antennae of a stonefly; the ephemereid mayfly's response is to bend its tail forward over its back in a "scorpion posture". This apparently fools the stonefly into thinking that the mayfly is too big to eat. When it come to finding prey by touch, however, the octopus is king, using its long tentacles to explore crevices and capture its prey.

## Prey Capture by a Damselfly Larva

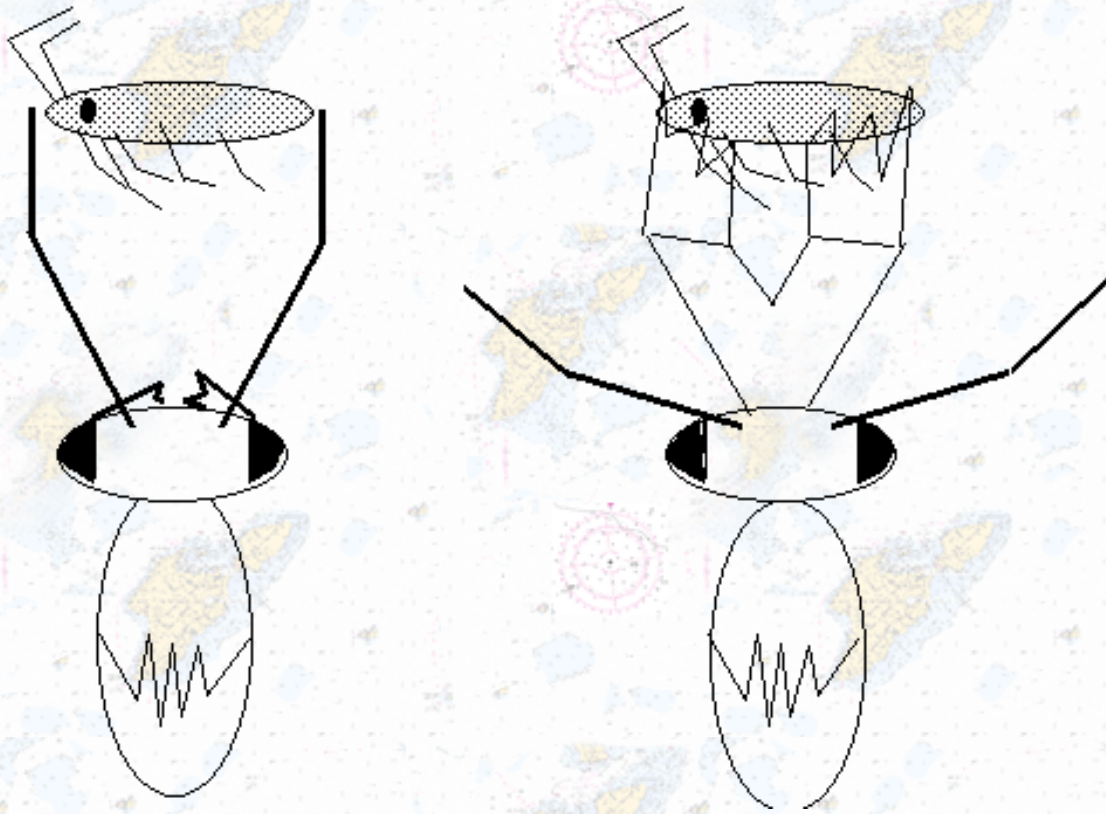
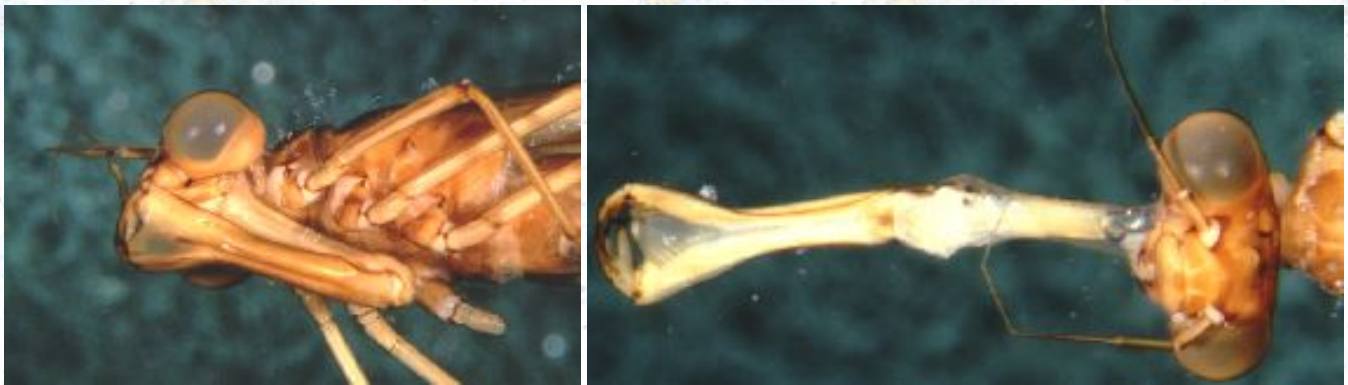


Figure 3. Capture of an amphipod by a damselfly larva. When the amphipod is detected between the two antennae (above, left), the antennae spring back and the labium is shot forward to grasp the prey (above, right). The labium is held folded under the head when not in use. In the images below, you can see the extent to which the labium can be extended in the damselfly *Archilestes grandis*.



Capturing prey often involves catching highly mobile prey, and a number of aquatic predators are very swift. We term predators that actively search out mobile prey as *pursuit predators*. These organisms seek out their prey, which may in turn also be quick. Pursuit predators are thus distinguished by being fast and having good distance senses; common examples would be sharks. There are other strategies, however. *Searchers* are highly mobile themselves, but search out sedentary prey. Examples here might include many starfish; and it is really a minor distinction between searcher-predators and searcher-herbivores, which also must seek out a sedentary food source. Search strategies employed by both predators and herbivores are currently a "hot" area of research. *Ambushers* take a different tack. They are sedentary, and lie in wait for mobile prey. Many dangle a lure of some sort to draw in the unwary. Alligator snapping

turtles, for instance, dangle a worm-like extrusion from their tongues. Perhaps the best in this vein, however, are certain freshwater mussels that modify a portion of their mantle to resemble the females of certain species of fish (Figure 4). When an unsuspecting male fish approaches, the mussel squirts out a cloud of larvae, which attach themselves as ectoparasites on the gills of the fish (Figure 5).

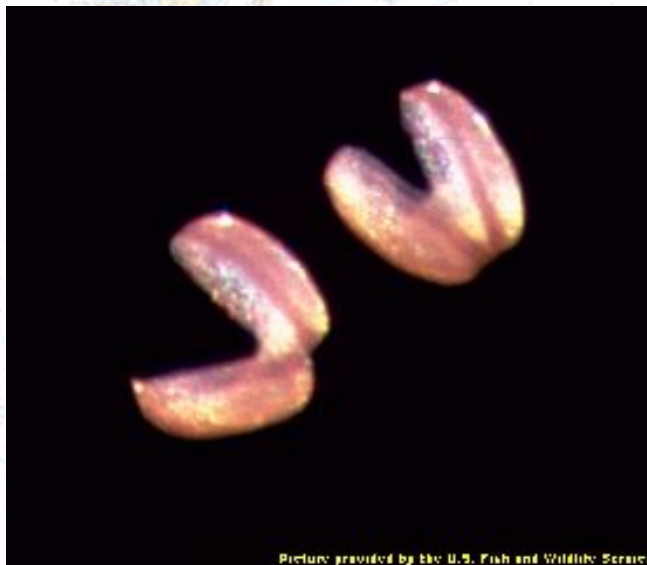


Figure 4 (left) Mantle of a mussel adapted to resemble a fish. Figure 5 (right) Glochidia (larvae) of a mussel. These organisms clamp down on the gills or fins of a fish, and draw nutrients as ectoparasites on the fish. They drop off after a few weeks, and usually do not seriously injure the fish.

Prey may be captured by use of a number of structures. Many organisms simply engulf their prey with the mouth. Fish and turtles are especially good at this; the prey is overcome through a combination of lunge and suction. The seahorse and its relative the pipefish also use suction to capture their prey. Other organisms use tentacles or other appendages to seize prey. Among the latter the preying-mantis like forelegs of the mantid shrimps are particularly interesting. Adapted variously to slice, crack, or snatch prey, they are among the fastest moving structures in water. One species, which uses knobs on the ends of the forelegs to crack open mollusk shells, can hit with an impact equivalent to a .22 caliber bullet (they can and have cracked aquarium glass, making them fun to tease at major aquariums). Dragonflies and damselflies use an extensible labium to capture prey.

Once captured, the prey must be overcome. In many instances, this is simply a matter of bolting it down, that is, swallowing it whole and alive, and allowing the digestive juices to go to work. In other cases, various structures are used to tear or cut up the prey before it is swallowed. Octopuses and squids have beaks that tear prey and inject a poison. All *marine* snakes are poisonous as well, injecting a poison similar to that of the cobras. Arthropods generally have tearing or cutting structures associated with the legs; examples would include the chelipeds of lobsters and crayfish, or the gnathopods of horseshoe crabs. Starfish that prey on bivalve mollusks wrap themselves around the clams and pry it open just enough to evert their stomach into the shell cavity, where it excretes a poison and digestive juices that digest the unlucky mollusk within its own shell. Mollusks are not defenseless, however; cone-shell gastropods are quick enough to lunge at small fish and overcome them with a toxin, and some snails use their radula to bore through the hard outer cases of barnacles and bivalves.

Suctorial feeding, where the juices of the prey are sucked out, is also common in water. Aquatic insects in the order Hemiptera, such as water striders, water boatmen, giant water bugs, and water scorpions, all feed in this manner. Likewise, leeches and lampreys latch onto their prey and suck out the juices. This type of predation is often called *ectoparasitism*. The whole phenomenon of parasitism can be considered as a subset of predation. To distinguish a predator from a parasite, several things can be considered, but remember, as in all continua, the lines separating these two modes of life often blur. Usually, but not always, predators tend to be bigger than their prey, while parasites tend to be smaller than their hosts are. Predators almost always kill from the outside and engulf their prey; parasites may be external or internal, and usually do not directly ingest host tissue other than blood. Many parasites simply live in the guts of their hosts and absorb food from the surrounding fluids. Parasites often have degenerate systems, especially sensory systems, mouthparts, and digestive systems, and parasites often show complicated life cycles with alternating hosts and an emphasis on reproduction. Predators almost always kill their prey in the act of predation, while a "good" parasite usually does not kill its host directly, although it may weaken it or leave it open to infection. *Parasitoids* are insect endoparasites, usually of other insects, that differ from other parasites in that they usually do kill their prey. Insects can get away with this because they reproduce so rapidly. In aquatic systems there are some tiny wasps which "fly" underwater to parasitize other insects. Both hunters and parasites consume high-quality food and thus have simple, short guts.

#### Grazers and Browsers:

As already mentioned, these organisms really act much like a searching-type predator in that they are mobile and search for a sessile "prey" (in fact, many organisms in this group really don't distinguish between plant and animal food - whatever they can shovel in their mouths). The common problems they face are finding the patches of food and removing it from the substrate.

Many herbivores are highly mobile swimmers with great maneuverability. They must be able to "hover" over a site while removing food, and often must get into tight spaces where algae may be attached. Other herbivores crawl over the bottom to patches of algae. Once the food is found, hard structures must be brought into play as has already been discussed. Even at this point, however, these organisms still have formidable obstacles to overcome. Many plants defend themselves with poisonous chemicals and indigestible bulk such as cellulose that makes them nutritionally unappealing. Herbivores may counter by careful, selective feeding on only those plants with the fewest chemical defenses, with elongate guts so that material may be digested better, and with symbionts bearing the necessary enzymes to digest cellulose and other materials that the herbivore cannot digest on its own. There is a constant evolutionary "arms race" as herbivores try to overcome the new defenses that are always arising among plants.

### **Avoiding Predation**

The evolutionary war between plants and herbivores is also being fought between prey (both herbivores and carnivores) and their predators. Any potential prey will try to avoid being eaten, and the predators must overcome these defenses. Basically, there are three main tactics the prey can try - to increase search time, increase handling time, or actively repelling the predator. The first two rely on some economic-ecological principles, the first being that time is like money (economics) or energy (ecology). If the predator requires too much time to successfully capture and eat a prey item, it will leave that species alone in the future. It doesn't do the individual any good, but it may help out that individual's offspring.

Increasing search time is another way of saying hiding. You are no doubt aware of the cryptic patterns exhibited by organisms that makes them hard to see. These organisms often have various protuberances to help break up their body outline, and are colored to resemble their surroundings. Some of the best examples are the various organisms found in the drifting seaweed *Sargassum*. Some organisms take a slightly more active role; the decorator crab actively finds anemones and other sessile organisms and encourages them to grow on its shell, helping to camouflage it (those stinging tentacles don't hurt either!). Stripes and fake eyespots on many aquatic organisms also help to confuse predators and divert their attacks away from critical areas.

Increasing handling time can be done in a number of ways. Schooling fish are easily found but hard to capture since their numbers confuse predators. Shells, especially those with ridges or spines that effectively increase their size without increasing the weight proportionately, make it tough for a predator to get to the nutritious parts of the animal. There is often a close correspondence between the size of the shell and the size of the predominate predators' jaws (claws, gnathobases, whatever).

Active defenses include attacking the predator directly, either alone or in concert with others of your species. Predators, of course, have the necessary weapons at hand for such attacks, but many herbivores can improvise effectively. Running is a type of active defense, and it is often enhanced by trickery, such as leaving a severed (but replaceable) limb to distract the predator, or squirting a cloud of ink or other chemicals in its path to confuse or irritate it. Other means of active chemical defense may be widespread in aquatic systems, but if they are, they are poorly known as compared to the myriad of chemical defenses exhibited on land. Many examples of chemical defenses are known from insects, perhaps it is because the insects are not one of the dominant aquatic taxa that we do not see more examples of chemical defenses in aquatic systems.

### **Microhabitats and Feeding**

Often, the microhabitat that an organism inhabits is closely tied to its feeding. Scrapers will be found on top of rocks where algae grow, while deposit feeders will be found in eddies near the bottom where detritus settles out. Filter feeders will gather where the currents are strong, and predators will be found everywhere. The two figures below (Figs. 6 & 7) illustrate somewhat the complex environment that develops in aquatic systems.

# Food sources in a stream

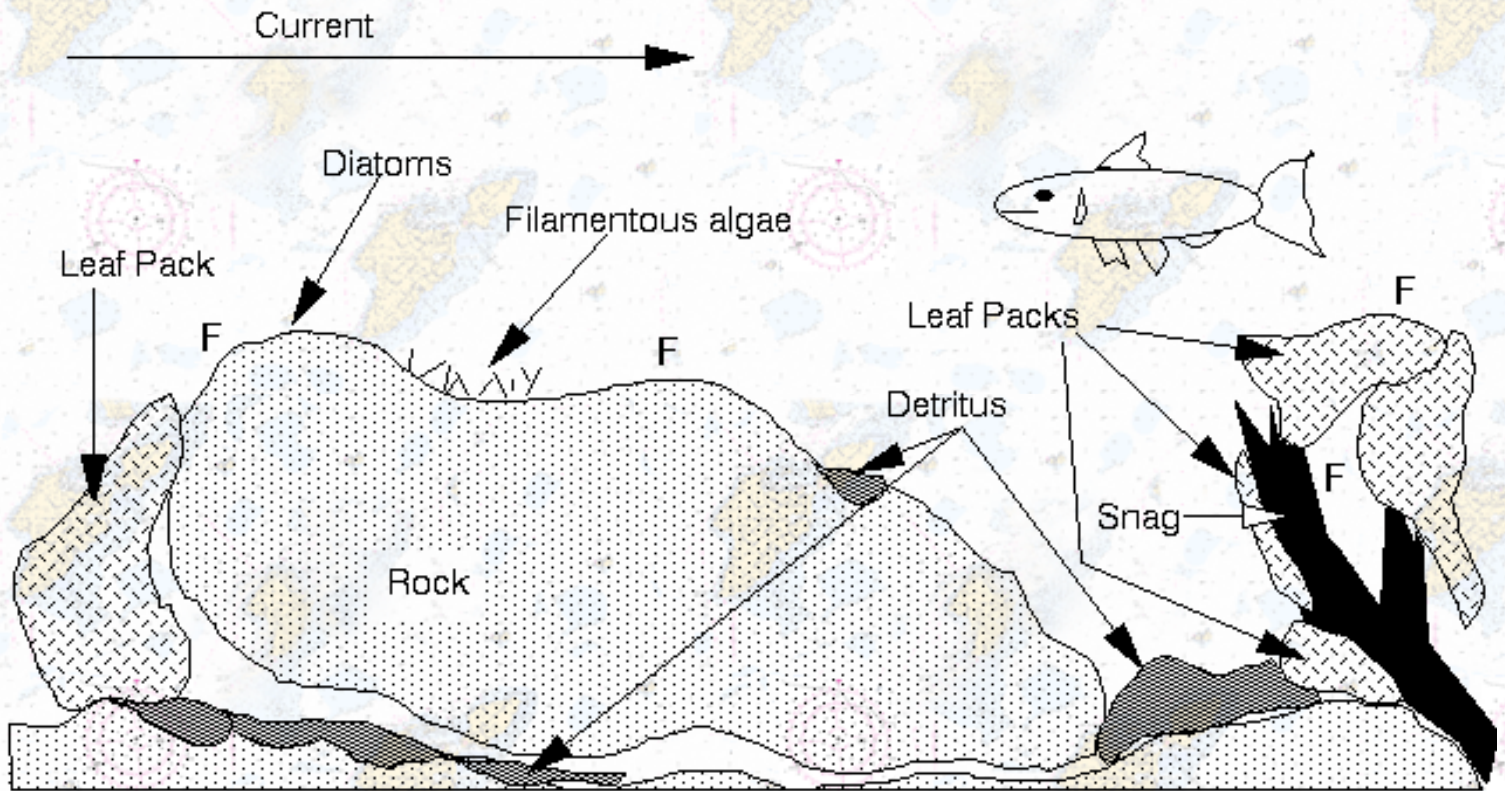


Figure 6. Microhabitats in a stream. Scrapers will be found on the open rock faces, while filters move to areas where they can intercept the current (F). Deposit feeders will be found in the crevices under the rocks and among the detritus. Shredders will occupy the leaf packs, and numerous detritivores will inhabit burrows in the bottom sediments. Miners may inhabit the wood of the snag. Predators will be found (in lesser numbers) in all these microhabitats. Most of the niches are filled by aquatic insects with some representation by other phyla.

# Food sources on the Coral Reef

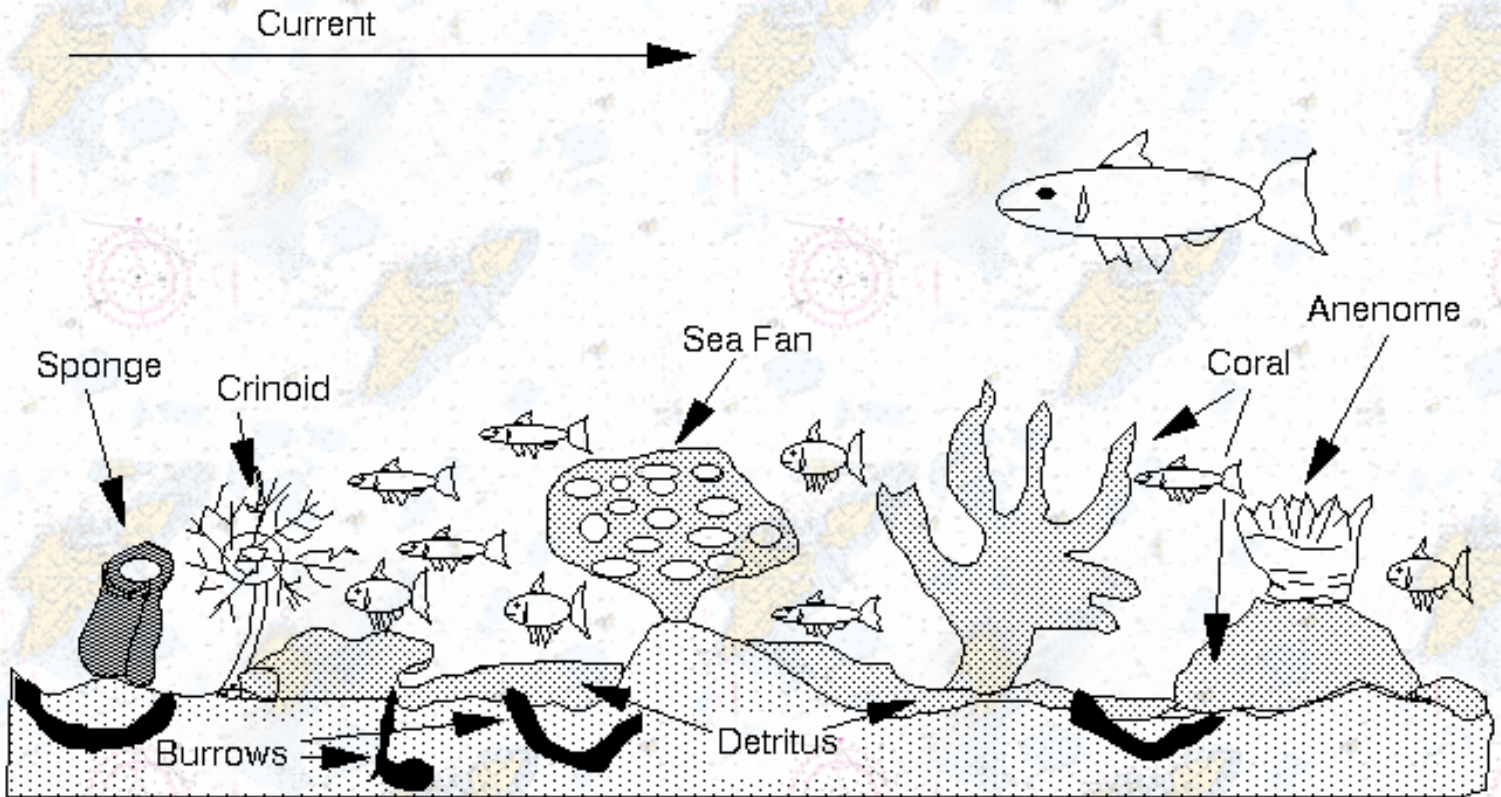


Figure 7.. Food sources on a coral reef. Photosynthesis occurs on all exposed surfaces, and many of the organisms such as sponges, sea fans, coral, and anemones also house photosynthetic endosymbionts. As in the stream, detritivores of various types live under rocks and coral and come out to feed on deposits. A number of organisms are adapted to either filter out material from the water (sponges, corals, sea fans), or intercept it before it is deposited (crinoids). Predators are found throughout the system. As opposed to freshwater systems, where fish are primarily predators, fish on a coral reef fill a variety of niches, and other niches are filled by members of various phyla, particularly annelids, crustaceans, echinoderms, and mollusks.

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# About the Sextant....



A sextant is a device used to determine location. Specifically, it allows one to determine at what angle the sun or other stars are above the horizon. Armed with this and the date, one can determine latitude. The sextant was a valuable tool used by navigators on the ocean. This incarnation is likewise intended as a navigation device, helping the student to find her or his way through the subject of aquatic biology. It is combined with another textbook in Aquatic Biology (Biology 450) at Marietta College.

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The Sextant was written by Dave McShaffrey in 1989 (although it wasn't called The Sextant then). It has been revised several times since. In 1997, when it was time to produce the study guide for the class, a problem arose. The files were WordStar 6.0 files; there was no computer handy with WordStar. It meant either loading WordStar (all those disks) or converting the files to a newer standard. While WordStar (and NewWord before it) was an admirable word-processing program, it was time to move on, and this hypertext document is the result. A further update was completed in 2001-2002

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