Marine Plankton Ecology --- A New Perspective

We are members of the terrestrial world. Thus, we are more familiar with terrestrial ecosystems based on our daily experience, and text books often use terrestrial life forms to introduce various concepts and principles in ecology. However, the aquatic habitats are drastically different from terrestrial habitats. Many of the basic characteristics of an organism, such as its morphology, locomotion, nutritional mode, life history, etc., depend on the medium (air or water) in which the organism resides. Thus, by comparing the basic physical properties between air and water, one can unveil many of the unique characteristics of aquatic ecosystems.

- Water is ~1000 times denser than air, and the density of most biological objects are in the range of 1050 to 1200 kg m^{-3}; thus, aquatic organisms enjoy the benefits of buoyancy support whereas terrestrial organisms have to work against gravity.
- Higher density results in a higher pressure drag as an organism moves through the medium (think of it as resistance to the organism's movement).
- Light attenuation is negligible in air, whereas light intensity decreases exponentially as it travels down the water column.
- Water is the best solvent on earth. Life processes are impossible without water.
- Oxygen diffusion is about 10,000 times faster in air than in water.

Such differences lead to several key contrasts between terrestrial and aquatic ecosystems. The following list is to provide you with some general ideas how organisms cope with the different environments, and the ecological consequences. It is not meant to be exhaustive, and you may think of exceptions to each case. Nevertheless, this document should help you put "plankton ecology" in a new perspective.

Terrestrial:

- Organisms tend to "sink" to the bottom such that the terrestrial biosphere is compressed to a 2-dimentional space; i.e. the earth surface. "Plankton" do not exist on land. There are also no nekton for that matter.
- Organisms need to invest energy and material to work against gravity. As a result terrestrial organisms have evolved prominent support mechanisms, notably the vascular system in plants, endo- and exo-skeletal and muscular systems in animals.
- Because of gravity, the "biological landscape" begins from the bottom up. Plants compete for light by growing taller and wider. However, that also requires increasingly bulky support mechanisms.
- Cost of support in plants is reduced by using refractory, long-lasting materials such as cellulose and lignin.
- Because of the need for a massive and rigid support system and the high cost of movement, terrestrial plants invariably lack motility.
- Because the primary producers are non-motile, the only way a consumer will get to them is by moving itself. That's why sedentary or sessile consumers do not exist on land.

- Locomotion on land is mainly work against gravity; aerodynamics is a non-issue for most organisms (think of your posture when you move through air vs. water).
- Because land plants contain high amounts of refractory materials, consumers need special body physiology and behavior to be able to feed on them; e.g. morphology and continuous growth of teeth, digestive tract structure, cellulolytic symbionts, regurgitation, production of pseudo-feces. Results: the evolvement of a highly specialized nutritional mode in terrestrial system: herbivory.
- Because of the high cost in support and transport, thermodynamic loss between trophic levels tends to be high on land, resulting in food chains typically no longer than 3 trophic steps.
- Because land plants don't move, evolution of allelopathy is more likely.
- Dead tissues and animal wastes stay on the ground where remineralization takes place.
- Land plants develop special vascular systems to take up dissolved nutrients and water from the ground. Because remineralization takes place in close proximity, nutrient depletion is less a concern; rather primary production is often regulated by water supply.
- The need for complex and specialized vascular and support systems requires that the dominant primary producers on land are multicellular organisms, and that they have a complex and long life cycles.
- Because of negligible light attenuation by air, herbivores avoid predators by herding, seeking physical refuge during the day, or becoming nocturnal.
- Little danger for terrestrial habitats to become anoxic. (Air density does decrease with altitude.)

Aquatic:

- Organisms can take advantage of buoyancy and suspend in water such that the aquatic biosphere is a 3-dimentional world. "Plankton" is as common as stars in the sky.
- Organisms need to invest little energy and material to work against gravity. As a result many aquatic organisms do not have prominent support mechanisms. Gelatinous and soft bodies are very common.
- Because of light attenuation in water, the "biological landscape" begins from the top down (except for shallow and vent systems). Phytoplankton reach for light by staying afloat. However, sinking rate tends to increase with size. As a result, phytoplankton tend to be small (Scale: land plants – cm to m; phytoplankton – μm).
- Cost of support in plants is minimal. Cell covering is mainly for protection or enhancing buoyancy. Some phytoplankton species lack cell wall.
- Because the organisms are not constrained by a massive support and vascular systems, motility (although limited) among phytoplankton is common (by flagella).
- Because phytoplankton are suspended in the medium, it is possible for consumers to reach them not by moving but by creating a <u>feeding current</u>. That's why sedentary or sessile consumers are common in water. Feeding current is only possible in aquatic habitats because of the high viscosity of water. Feeding current doesn't work on land (no land animals feed like a vacuum cleaner). During a part of their life cycle sedentary or sessile consumers produce planktonic form for dispersal (usually the larvae); hence the existence of meroplankton.

- Locomotion in water is mainly work against viscosity (small organisms) and drag (large and fast organisms). All large, fast moving aquatic animals have evolved a stream-lined body form.
- Because phytoplankton contain relatively small amounts of cellulose, consumers may not need special body parts or physiology to be able to feed on them; thus, the distinction between nutritional modes is less restrictive in aquatic ecosystems, and omnivory appears to be the norm among plankton.
- Because of the relatively low cost in support and transport among plankton, thermodynamic loss between trophic levels tends to be low, and food chains with more than 3 trophic steps are very common.
- Because phytoplankton aren't fixed in space, evolution of allelopathy is less likely.
- Dead tissues and animal wastes tend to sink to the bottom where remineralization takes place, hence the issues of "biological pump" and "upwelling" are unique to nutrient dynamics in aquatic ecosystems. Because phytoplankters are suspended in water, desiccation is not a concern; rather nutrient depletion is a more important factor regulating primary production.
- Phytoplankton absorb dissolved nutrients through diffusion from surrounding water.
- The lack of complex body structures allows most phytoplankters exist as unicellular or simple colonial organisms, and that they have simple and short life cycles (reproduce by simple cell divisions).
- The simple and short life cycle of most phytoplankton allow them to increase in population rapidly under favorable condition; hence the phenomenon of blooms and "red tides".
- Because the aquatic primary production is dominated by small phytoplankton cells, and because consumers do not need complex physiology to feed on these cells, consumers can remain as small and simple organisms. Phytoplankton in the ocean is mainly consumed by unicellular organisms, i.e. protozoans, which can also reproduce rapidly and keep pace with phytoplankton. The dominance of unicellular life forms among both primary producers and consumers are unique to aquatic habitats. Because of the small size of phytoplankton cells, they are usually consumed whole, which is very different from grazing on land. As a result, "grazing" in the aquatic world is equivalent to certain death of the primary producers. This calls into question about the evolution of "anti-grazing" intracellular chemical defense (which is common among land plants where grazing is non-lethal).
- The water column generally lacks physical structures that zooplankton may use as refuges. However, because of light attenuation in water, zooplankton may seek protection by being small, being transparent, or going deep during daytime.
- Because of slow diffusion of oxygen in water, oxygen depletion is a serious concern for organisms. Hypoxia is a common phenomenon in coastal and stagnant waters. The widespread existence of anaerobic life forms (mainly microbes; facultative or obligate) and the ability to tolerate low oxygen condition is unique to aquatic organisms.

Table 4.1 The density at one atmosphere of air, fresh water, and seawater.

T (°C)	Density, ρ (kg m^{-3})		
	Air	Fresh Water	Seawater (S = 35)
0	1.293	999.87	1028.11
3.98	1.274	1000.00	1027.77
10	1.247	999.73	1026.95
20	1.205	998.23	1024.76
30	1.165	995.68	1021.73
40	1.128	992.22	1017.97

Dynamic viscosity of air, fresh water and seawater.
(from Table 5.1 in Denny 1993)

T (^{0}C)	Dynamic viscosity (N s m^{-2}) (= kg s^{-1} m^{-1})		
	Dry air	Fresh water	Seawater (S = 35)
0	1.718×10^{-5}	1.79×10^{-3}	1.89×10^{-3}
10	1.768	1.31	1.39
20	1.818	1.01	1.09
30	1.866	0.80	0.87
40	1.914	0.65	0.71

Table 4.4 The densities of various inorganic and biological materials.

Material	Density (kg m^{-3})
Inorganic Materials	
Pure water	1000
Seawater	1025
Calcium carbonate	
Calcite	2700
Aragonite	2900
Calcium phosphate	
Apatite	3200
Glass	2400 to 2800
Aluminum	2700
Iron	7870
Organic Materials	
Coral skeleton	2000
Mollusk shell	
Gastropod shell	2700
Nautilus shell	2700
Bivalve shell	2700
Crustacean Shell	1900
Insect exoskeleton	1200 to 1300
Sea urchin spines	2000
Bone	
Femur (cow)	2060
Whale ear bone	2470
Tooth enamel	2900
Muscle	1050 to 1080
Fats and oils	915 to 945
Wood	
Red oak	680
Sweet gum	1000
Lignum vitae	1300

Comparison of approximate values for air (at 1 atm) and sea water at 20°C. The values are approximate and are from Sverdrup et al. (1942), Gray (1957), and Prosser and Brown (1961).

	Density (g cm^{-3})	Viscosity (g cm^{-1} sec^{-1})	Diffusion constant for O_2 (cm^2 sec^{-2})
Sea water	1.02	1.1×10^{-2}	2×10^{-5}
Air	1.20×10^{-3}	1.8×10^{-4}	2×10^{-1}
Water-to-air ratio	850	60	10^{-4}

Further readings:

Denny, M.W. (1990) Terrestrial versus aquatic biology: the medium and its message. Amer. Zool. 30: 111-121.

Denny, M.W. (1993) Air and Water: the Biology and Physics of Life's Media. Princeton.

Strathmann, R.R. (1990) Why life histories evolve differently in the sea. Amer. Zool. 30: 197-207.

Vogel, S. (1988) Life's Devices, the Physical World of Animals and Plants. Princeton.