Zooplankton
Chapters 6-8 in Miller for more details

I. Major Groups

Heterotrophs—consume organic matter rather than manufacturing it, as do autotrophs.

Zooplankton can be:
- herbivores
- carnivores (several levels)
- detritus feeders
- omnivores

Zooplankton, in addition to being much smaller than familiar land animals, have shorter generation times and grow more rapidly (in terms of % of body wt / day).

1. Crustaceans- include shrimp, copepods, euphausiids ("krill")

Characteristics: Copepods, euphausiids and shrimp superficially resemble one another. All have:
- exoskeletons of chitin
- jointed appendages
- 2 pair of antennae
- complex body structure, with well developed internal organs and sensory organs

Habitats: Ubiquitous.
- Euphausiids predominate in the Antarctic Ocean, but are common in most temperate and polar oceans.
- Copepods are found everywhere, but are less important in low-productivity areas of the ocean - the "central ocean gyres". They are found at all depths but are more abundant near the surface.

Role in food webs:
- Euphausiids and copepods are filter-feeders. Copepods are usually herbivores, while the larger euphausiids consume both phytoplankton and other zooplankton.
- Shrimp are usually carnivores or scavengers.

2. Chaetognaths - ("Arrow worms")

Characteristics:
- 2-3 cm long
- wormlike, but non-segmented
- no appendages (legs or antennae)
- complex body structure with internal organs

Habitat: Ubiquitous
Role in food web: Carnivore feeding on small zooplankton such as copepods.

3. Protozoan - Include *foraminifera, radiolarians, tintinnids* and *"microflagellates" ca. 0.002 mm*

Characteristics:
- Single-celled animals.
- Forams have calcareous shell.
- Radiolarians have siliceous shell.
- Both Forams and Radiolarians have spines.

Habitat: Ubiquitous
- Radiolarians are especially abundant in the Pacific equatorial upwelling region.
- Protozoa are especially important components of the food web in low-productivity ocean areas.
- Both are found in sediments as well as in the water column.

Role in food web: Feed on small phytoplankton, bacterioplankton, and other protozoans. They can be bacteriovores, herbivores, or carnivores.

4. Gelatinous Zooplankton: includes a variety of fragile, jelly-like organisms which are not closely related taxonomically.

*Cnidarians*: jellyfish

Characteristics:
- Very simple body structure, with 3 layers: inner membrane, jelly, and outer membrane.
- No internal organs but have a digestive cavity.
- Have stinging cells on their tentacles called nematocysts.

Habitat: Found everywhere and at all depths. More abundant in surface waters.

Role in food web: Carnivores, trap prey in tentacles.

*Ctenophores*: "comb jellies".

Characteristics:
- Also have a simple body structure without internal organs.
- Move by means of cilia.
- Sometimes have 2 long tentacles.
- Are often bioluminescent.

Habitat: Found everywhere

Role in food web: Carnivores, predators.

*Salps*: A type of *tunicate*.

Characteristics:
- Members of the phylum Chordata.
- Have a complex body structure including internal organs and a nervous system as larvae but are "degenerate" as adults.
- May be solitary or colonial.

Habitat: Warm surface waters. Rare at high latitudes.

Role in food web: Largely feeds on phytoplankton. A "ciliary-mucous" filter
feeder.

**Overall:** Gelatinous zooplankton are very important, but little-studied because of sampling problems; they often disintegrate in nets or other sampling devices.

### 5. Pteropods

**Characteristics:**
- Mollusks related to snails.
- Small, ~ 1 cm long.
- May or may not have a conical shell.
- Move by means of "wings" (modified foot).

**Habitat:** Found everywhere

**Role in food web:** May be herbivores or carnivores. Filter-feed using a "mucous net".

### 6. Meroplankton

*Meroplankton* are organisms which are part of the plankton for only part of their life cycle, usually an early, larval stage.

As adults the meroplankton are benthos (including intertidal organisms) or nekton.

The meroplankton often do not resemble the adult forms, to the extent that some were once thought to be separate species.

Meroplanktonic larvae promote survival of the species:
- Currents carry the offspring to new areas, especially important for sessile (immobile) benthic animals. Thus, the offspring do not compete with the parents for scarce resources such as food or space. Also, local "disasters" will not wipe out all close relatives.
- Meroplankton live in surface waters where food is abundant. Sometimes, the habitat of the adult would not have enough food, especially for a very small organism that could not effectively use the feeding strategy (for example, predation, filter feeding) of the adult.

Meroplanktonic larvae also have disadvantages:
- Often, reproduction occurs to coincide with the spring bloom and abundant food. If the spring bloom is not "on time", meroplankton may starve.
- Meroplankton are food for the many predators on plankton.
- The currents may not carry the meroplankton to an area that provides suitable conditions for adults.

Therefore, organisms which have meroplanktonic larvae usually produce hundreds or thousands of eggs, so that a few will survive.
Although there are a great many groups of zooplankton in the oceans, we focus on 3-4 main components:

1) microzooplankton (less than about 10 µM)
   a. important in the microbial web
   b. composed of (primarily) flagellates, ciliates, and other protista

2) Euphausids (krill)
   a. Important because of their role in fisheries
   b. Dominant in California coastal waters

3) Copepods
   a. We know the most about these organisms
   b. Dominant grazers of diatom-dinoflagellate-coccolithophore blooms, so tend to be studied more

4) Other major groups
   a. Chaetognaths—a major link in some fisheries food chains
   b. Jellies—of increasing importance because they seem to serve as an “indicator” group for change (‘the rise of slime’)

II. Measuring Zooplankton Biomass

- Because zooplankton have behavior and are mobile, they are much harder to quantify than phytoplankton, which are largely passive. This has been a fundamental challenge in biological oceanography, and still isn’t resolved.

- We tend to catch the “slow, stupid, and blind” organisms, because those are the ones that can be entrained in nets.

- Behavior also means that zooplankton are “patchy”, or not uniformly distributed, in the environment. Despite this, we still refer to their concentrations on a unit volume basis (zooplankton per cubic meter, for example).

- Microzooplankton are a special case…small enough to be considered passive particles, they are caught and enumerated using the same methods as for phytoplankton. However, they are very fragile, so great care must be taken not to destroy them during sampling.

A. Nets

Still the most common method for enumerating zooplankton. Size fractions are determined by the size of the net (333 and 505 microns, for example). Samples are often preserved, and estimates of mass are determined as either biovolume, gram carbon equivalent, or a direct count of the groups (e.g. numbers of copepods)
Bongo Nets: used for a vertically integrated sample from depth to the surface. The pairs of nets can be either different sized mesh, or replicate samples

Ring Nets: similar to bongos, but a single net. The size (ring) and mesh vary depending on what is being collected. Typically used vertically or obliquely (towed at an angle).

MOCNESS: Multiple Open and Closing Net Environmental Sampling System. Same idea, but has multiple open and closing nets so that different layers of water can be sampled without having to change the nets, etc.

Longhurst Hardy Plankton Recorder: towed instrument with two layers of gauze that continuously “sandwiches” particles and stores them in a drum. It provides a record of what was in the water column, and has the advantage of not integrating everything (so individual organisms can be identified as a function of where they were collected)

B. Indirect Estimates

OPC: Optical Plankton Counter. Doesn’t collect samples, but instead sizes and counts the zooplankton by allowing the plankton to pass through an illuminated chamber (similar to a flow cytometer for phytoplankton)

ADCP: Acoustic Doppler Current Profiler. This is an echosounder that sends pulses of sound into the ocean, which bounce off hard objects. Zooplankton can be estimated if the correct frequency (which determines size of the object being measured) is used, and if some assumptions about body density are made. Note that it doesn’t actually count zooplankton…it gives a signal that must be interpreted in terms of biovolume or numbers.

III. Rate Measurements

As with phytoplankton, the biomass doesn’t tell us very much, other than who is there. We generally want to know how fast they are growing, and what their consumption of phytoplankton is.

Clearance Rate: volume of water filtered per unit time. Assuming no replacement of the phytoplankton, the phytoplankton will be consumed following an exponential relationship.

Ingestion Rate: The average individual rate of consumption (ingestion) after taking into account changes in prey density, and integrating over some finite time period.
Generally, there is some threshold or saturation function, which copepods reach when food is plentiful. Once that is reached, Clearance Rate decreases to keep Ingestion Rate at the optimum level (i.e. the zooplankton slow down their feeding to maximize intake).

Optimal Ingestion Rates depend on a number of factors:
1) Temperature (metabolic activity)
2) Gut Clearance Rate (how fast the food is metabolized)
3) Prey preference (is it nutritionally valuable?)

To measure zooplankton grazing, we can look at the processes of interest: we want to estimate clearance and ingestion. The easiest way to do this is to simply see how long it takes a known population of zooplankton to consume their prey:

1) Measure the disappearance of algae (prey) versus time
   a. Need to account for in situ growth of prey
   b. Advantages: very easy calculation
   c. Disadvantages: Need to do it in a bottle (so no losses)
   d. Variations on this include using labeled beads rather than plankton (more control), or using fluorescently labeled bacteria (FLB) to estimate microzooplankton grazing

2) Chlorophyll Gut Contents
   a. To avoid keeping them in a bottle, can look at how much chlorophyll is in their guts at any given time, and how fast they clear their guts
   b. Collect zooplankton, split them into groups, and measure gut fluorescence as a function of time
   c. Assuming that the average gut content at time zero is representative, can calculate grazing rate
   d. Advantages: no bottle, can be done on natural populations, estimates both grazing rate and gut clearance rate
   e. Disadvantages: assumptions about chlorophyll not being assimilated, effects of handling, temperature, etc.

3) Mass Balance
   a. Assuming we can estimate phytoplankton growth, and it’s steady state, then we can estimate the fraction that must be grazed
   b. Sum up the carbon (for example) in the standing stock (biomass of zooplankton), the export flux (fecal pellets), and the production of DOC.
   c. Advantages: indirect estimate, can account for all carbon without measuring each rate
   d. Disadvantages: huge assumptions about steady state, biomass, etc.
How do we estimate zooplankton growth? There isn’t a simple method similar to chlorophyll, nor do they rely on photosynthesis.

1) Physiology
   a. We can use allometric relationships, and simply solve for growth as the change in population after taking into account respiration, mortality, reproduction, and ingestion.
   b. In reality, this IS REALLY HARD TO DO; it requires extrapolation from laboratory measurements, and is probably wrong
   c. Despite this, a common method is to apply a growth efficiency related to the grazing rate, and estimate secondary production based on food consumption and some assumed efficiency relationship

2) Change in biomass
   a. We can calculate growth by looking at individual species, and seeing how their biomass (or their developmental stage) changes through time
   b. As with phytoplankton, this only provides a net growth rate, and has all the same problems.

3) Recruitment
   a. Instead of trying to estimate growth of individuals (or populations), we can instead look at the rate of replacement
   b. Various methods for this: look at egg production (short time scales), number of individuals at each stage of growth (longer time scales), or number and size of adults in the population (muti-year)
   c. Knowing this, we can calculate an average growth rate for relatively large regions and long time scales

4) Temperature
   a. As with phytoplankton (Eppley), relationships have been found between zooplankton growth and temperature:

   \[ g = 0.0445 \, e^{(0.111T)} \]

   Where \( g \) is growth rate, and \( T \) is temperature
   b. This is very controversial, but probably holds true in a general sense. It is similar to Eppley’s or Behrenfeld-Falkowski’s model for phytoplankton growth.

IV. Behavior
Individual Behavior: zooplankton (copepods especially) are capable of rapid movement. They use this for at least three mechanisms:
1. Aggregation around prey (one source of patchiness)
2. Escape response when potential predators are encountered
3. “hop and sink” behavior is used to search out optimal conditions.
   a. When in high prey density (lots of food), they tend not to hop and sink as much
   b. When in low food conditions, their hop-sink behavior increases, until they find more prey
   c. They orient into the turbulent flow field, such that their hop-sink behavior also keeps them from moving to far laterally

Group Behavior (days): Zooplankton undergo diel vertical migration over the course of anywhere from 12-24 hours. Different species, and even different life cycles or times of year for a given species, modify this behavior to fit the needs of the population.

Advantages from DVM include:
1. Adaptive response to slow down metabolism (colder at depth)
2. Predator avoidance (migrate to the surface at night to avoid visual predators)
3. Predator avoidance (migrate to depth during night to avoid predators migrating the opposite way)
4. Laying eggs

Group Behavior (annual cycle): Zooplankton also undergo vertical migration on an annual cycle. This allows them to reach the mixed surface layer shortly after the onset of the spring bloom (in temperate latitudes), and to overwinter below the deep mixed layer in places such as the North Atlantic.