Ocea 130/230 Spring 2005
Biological Oceanography

Trophic Structure and Food Webs

Reading: Miller, pages 74-78, Chapter 5
Optional Reading: Valiela, Chapter 9
Optional Reading: Lalli and Parsons, pp. 112-136

I. Modeling Trophic Dynamics

- 1946, Riley predicted that you could determine the standing stock ("crop") of phytoplankton based on a combination of other factors. He used a multiple-regression model to determine that:

  $PP = 153t - 120P - 7.3N - 9.1Z + 6713$

  Where PP = phytoplankton biomass
  t = temperature
  P, N = phosphorous, nitrogen
  Z = Zooplankton

- 1947, He simplified this to a general mathematical model that stated:

  $dN/dt = N(Ph - R) - G$

  Where dN/dt = change in population of phytoplankton
  Ph = phytoplankton growth rate
  R = respiration
  G = grazing

- These models account for several factors:
  - "Bottom Up" Controls, e.g. Temperature, Nutrients, Light
  - "Top Down" controls, e.g. being eaten by someone else
  - "Trophic Cascades", e.g. if you increase nutrients, you increase phytoplankton, which causes an increase in zooplankton, and (eventually) an increases in fishes

- Within the model, all of the important factors, such as light and nutrient parameters, species dependency, etc. are accounted for by the sub-equations—Riley went on to explicitly include Michaelis-Menten kinetics, uptake versus irradiance, temperature dependence, respiration by grazers, etc.

- The Riley model can be combined with the concept of r versus K strategies:
  - We can divide all species based on their reproductive strategy
  - r strategists are opportunistic species, characterized by:
    - variable climate
    - small size

    - fast growth
    - not very competitive
  - K strategists are equilibrium species, characterized by:
    - constant climate
    - large size
    - slow growth
    - very competitive

- When combined with the size/density concept (review the Chisholm paper), we come up with the idea of a "food chain"

II. Food Chains

- Based on the Riley model, the classic food chain describes the transfer of energy from one group to the next
- Each level is a ***trophic group (or level)***, starting with primary producers—next level would be secondary consumers (herbivores), then tertiary, etc. ending with an ***apex predator***
- An important thing to remember is that the food chain is actually describing the transfer of ***energy*** as organic material, and it **only goes in one direction**
- With each step, following the r-K dichotomy, we expect size to increase, lifespan to increase, and abundance to decrease (the food pyramid idea)
- If we assume that the chain is really linear, we can predict a ***Transfer Efficiency:***

$$E_T = P_t / (\ _{t-1})$$

Where E is the efficiency, P is the <u>annual</u> production, and t, t-1 are the trophic levels we're looking at

  - In general, we assume about a 10% efficiency from one step to the next, meaning that 10% of the energy (or material) is transferred, 90% goes back to the environment (Sunlight to plant efficiency is on the order of 1%, plant to herbivore is on the order of 20%, every other step is about 5-20%)
  - This also explains the biological pump, which transfers about 1-10% of annual primary production to depth
- This also implies that we can model the availability, abundance, etc. of organisms based on our knowledge of the community production…for example, we should be able to predict a stable fisheries

III. Food Webs

- The preceding idea assumes that energy moves more or less linearly, and that there are relatively few organisms involved…the classic example from around here is that:

Physics -- > Diatoms -- > Krill -- > Blue Whales

- Things are rarely that simple, and you will usually be wrong if you try to model blue whale abundance (for example) based on the physics of California
- In the last 25 years, there's been a paradigm shift from the linear, food chain model to the complex (and complicated) food web model. This was caused by a combination of factors:
    1) New methods of measurement discovered new groups and abundances of organisms in the ocean
    2) We discovered that small organisms are very important!
    3) Microbial processes (rates) are equally important
    4) Bacterial abundance is much higher than previously thought
    5) The collapse of the major fisheries called into question our ability to mathematically model the transfer of energy

- This paradigm shift was initiated in 1977, when Hobbie published his method on directly counting bacterial cells in the ocean using Acridine Orange
    - As a side note, we don't usually use Acridine Orange any more, because it is fairly indiscriminate in labeling cells (dead or alive). The preferred stain is now DAPI, which only stains double-stranded DNA
- 1980's, Chisholm and Olson "discovered" prochlorophytes
- 1983, Azam coined the term "microbial food loop" to refer to the recycling of organic material independent of the classic food chain
- 1990's, Azam, Fuhrman, and others discovered the importance of marine viruses
- 2000's, the role of bacteria and viruses becomes increasingly important

Based on these findings, we now need to add several steps in the food chain:

1) Viruses
    - 0.02 – 0.2 microns in diameter
    - Approximately 10E6-10E9 per mL
    - they are species-specific, meaning they have a particular host organism, and won't attack species indiscriminately
    - Can account for 25-100% of phytoplankton mortality
    - Up to 50% of the phytoplankton might contain viruses at any given time

2) Bacteria
    - 0.2 – 1.0 microns
    - 10E5-10E8 per mL
    - On average, about 40-60% of primary production goes to bacterial respiration
    - They can use ***Dissolved Organic Matter*** (DOM) directly, attack other cells, or use inorganic nutrients
    - They can be extremely motile

Dissolved Organic Matter: this is functionally defined as anything that's organic (has a carbon chain) that passes through a filter, typically a 0.2 μm filter. Sometimes a GF/F glass fiber filter is used, which has a pore size of about 0.7 μm. DOM is made up of (typically):

DOC (dissolved organic carbon), including carbohydrates, lipids, proteins, etc.
DOP (dissolved organic phosphorous), including ATP, ADP, RNA, DNA, etc.
DON (dissolved organic nitrogen), including urea, amino acids, etc.

We don't usually care what, exactly, the compounds are, just that they are dissolved. Some of it is very long-lived (not easily used by organisms for food), and so there's a background concentration in the oceans, and also a more variable, "tasty" fraction that is constantly eaten/excreted by living organisms.

3) Heterotrophic Nanoflagellates
    - 10 – 10E5 per mL
    - Eat viruses, picoplankton, bacteria
    - Can control bacterial abundance, but only when they themselves aren't being controlled by another predator

4) Nano- and Microplankton
    - Dominated by protozoans, including ciliates, heterotrophic dinoflagellates
    - picoplankton (< 2 μm)
    - nanoplankton (2-20 μm)
    - microplankton (20-200 μm)
    - macroplankton (200-2000 μm)
    - megaplankton (>2000 μm)

At that point, we get into the organisms we're more familiar with…the larger phytoplankton, zooplankton, fishes, marine mammals, and humans.

IV. Trophic Pyramids

- We generally assume that there's about 10% energy transfer from one trophic level to the next, which helps explain why, on average, the size increases by a factor of 10-100 and the population decreases by a factor of 10-100 at each step

- However, in some parts of the ocean under the right circumstances, we can have ***inverted trophic pyramids*** where there's actually more heterotrophic respiration than there is autotrophic production

- On average, 50% of all photosynthetic material goes through the microbial food web, and gets "stuck" in the surface of the ocean rather than being sent to the deep ocean (the biological pump).

Take home message: The microbial food web is an incredibly important component that, until the 1970's, was virtually unknown. It accounts for a significant proportion of energy and material cycling in the oceans, and can keep much of the productivity "recycling" in the surface waters.

References of Interest (not required):

This is one of the first papers on inverted food webs across ocean basins

BUCK KR; CHAVEZ FP; CAMPBELL L. BASIN-WIDE DISTRIBUTIONS OF LIVING CARBON COMPONENTS AND THE INVERTED TROPHIC PYRAMID OF THE CENTRAL GYRE OF THE NORTH ATLANTIC OCEAN, SUMMER 1993. AQUATIC MICROBIAL ECOLOGY, JUN 27, 1996, V10(N3):283-298.

This is the paper discussing replacement of keystone species

Ernest, SKM; Brown, JH. Delayed compensation for missing keystone species by colonization. SCIENCE, APR 6, 2001, V292(N5514):101-104.

Interesting opinion article about the whole concept of keystone species

Davic, RD. Ecological dominants vs. keystone species: A call for reason. CONSERVATION ECOLOGY, JUN, 2000, V4(N1):U156-U157.

Review article on marine climate change and diseases (including Vibrio cholera)

Harvell, CD; Kim, K; Burkholder, JM; Colwell, RR; Epstein, PR; Grimes, DJ; Hofmann, EE; Lipp, EK; Osterhaus, ADME; Overstreet, RM; Porter, JW; Smith, GW; Vasta, GR. Review: Marine ecology - Emerging marine diseases - Climate links and anthropogenic factors. SCIENCE, SEP 3, 1999, V285(N5433):1505-1510.