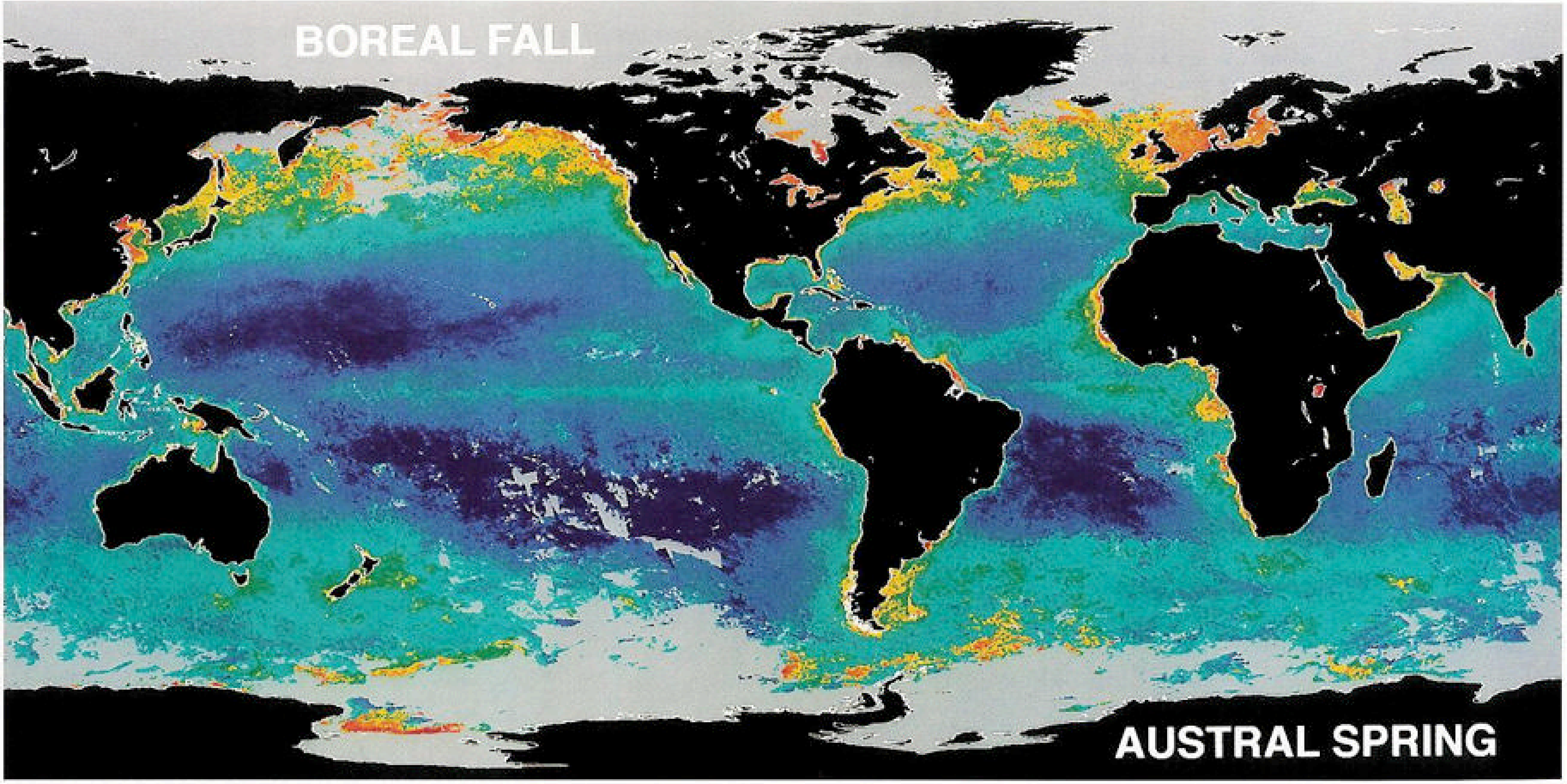
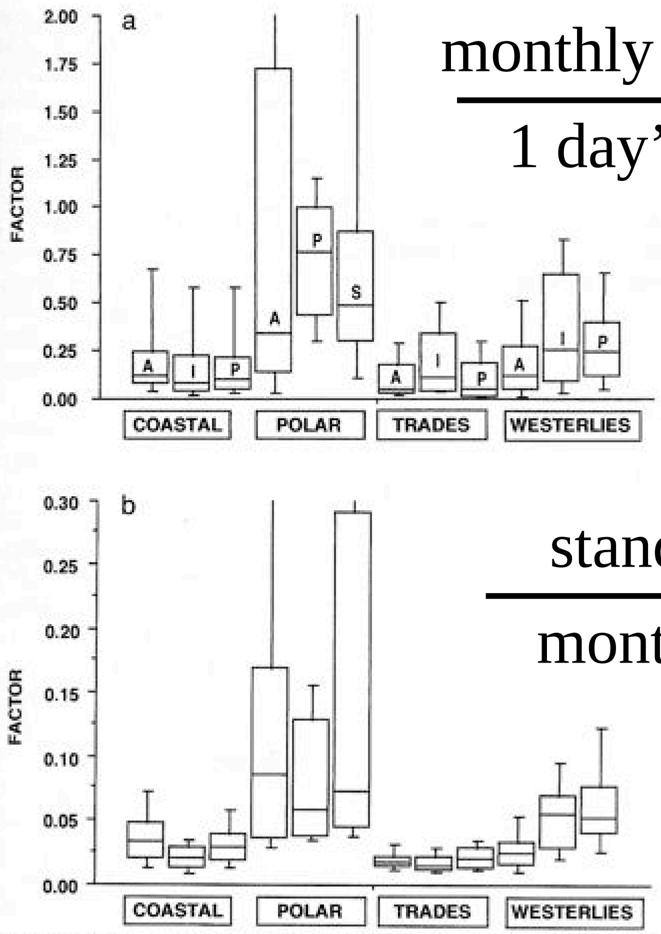


COLOR PLATE 2 Climatological (1978–1986) seasonal sea surface chlorophyll field obtained with Coastal Zone Color Scanner sensor for boreal fall (September–November). Color is a log scale for chlorophyll: purple = <0.06 mg Chl m^{-3}, orange-red = 1–10 mg Chl m^{-3}. Provided by NASA/Goddard Space Flight Center.

Why don’t chlorophyll distributions tell us the whole story?

Why study consumption?



monthly accum PP carbon / 1 day's 1° production

standing stock of PP / monthly 1° production

FIGURE 3.1 This figure shows how (i) monthly accumulation of phytoplankton carbon (top) is generally about one-half of 1 day's primary production and (ii) that standing stock (bottom) is equivalent to 0.02–0.10 of the monthly primary production or about one-half to 3 days productivity. The figure is based on CZCS data as described in the text; the analysis is split between oceans (A, I, P, and S) and biomes.

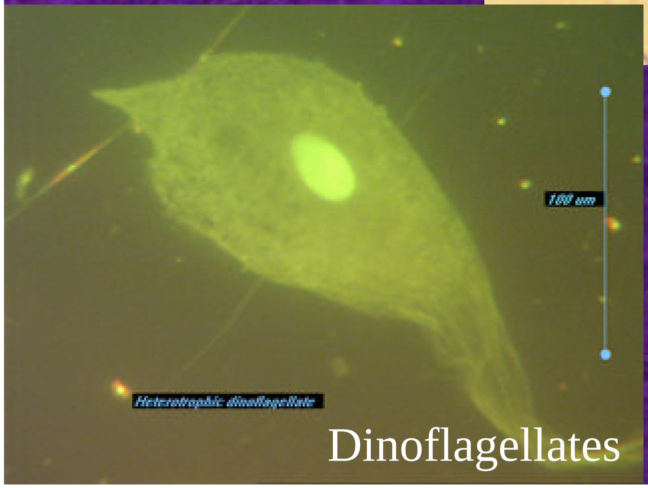
Longhurst 1998

- Standing stock is only a small fraction of production: need to understand consumption to get whole picture.

PP = phytoplankton

median: middle line of box
range: top & bottom bar

1° Consumers: Microzooplankton (Eukaryotes)



Protist grazers

- *a.k.a.* protozoans -- single celled organisms

Note: Protists can be autotrophs OR heterotrophs OR mixotrophs *(e.g., diatoms, coccolithophorids, dino-flagellates,"picoeukaryotes", etc.)*

NOT PROTISTS: *Prochlorococcus*, *Synechococcus*, other bacteria

2°Consumers

- Heterotrophic bacteria and archaea
  - DOC produced as a by-product of grazing*

  (1°consumers if growth is from direct phyto-exudation)

- Other protists (ciliates/dinoflagellates)
  - Many are omnivores (consume phytoplankton and heterotrophic organisms)

- Metazoans
  - usually metazoans are 3° consumers or higher, however

2°- 4° Consumers

Copepods -- most common (numbers and biomass)

Well-studied: easily caught with nets and seen with low power microscopes or the naked eye

Specialized feeding appendages

- Filter or Suspension feeders (usu. herbivores)
- Raptorial feeders (usu. carnivores)

Euphausiids (krill) -- Shrimp-like

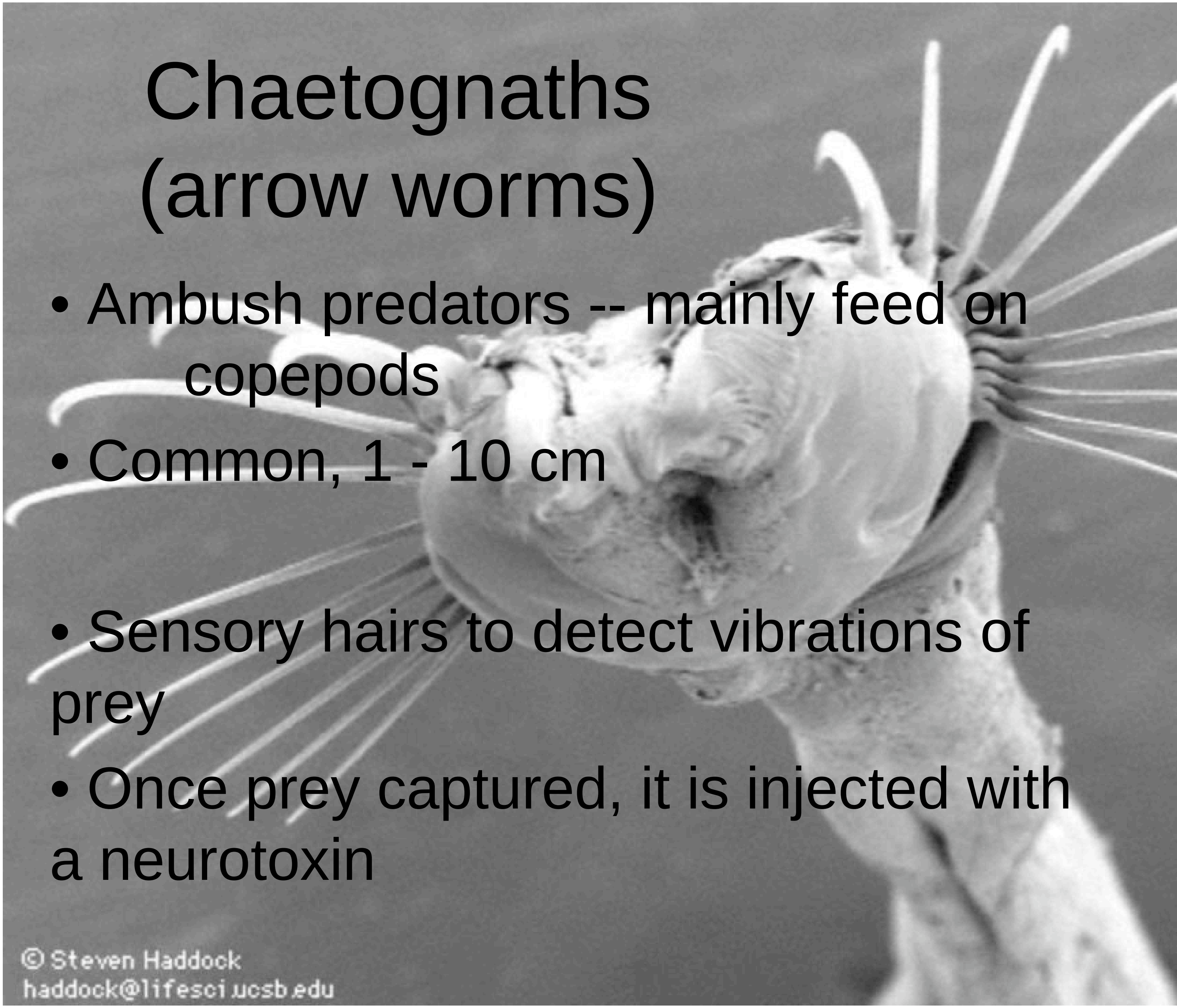
Some herbivorous, some carnivorous

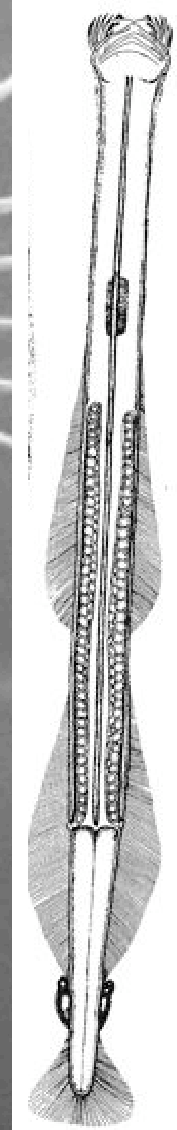
Significant populations in Antarctic waters

Chaetognaths (arrow worms)

- Ambush predators -- mainly feed on copepods
- Common, 1 - 10 cm

- Sensory hairs to detect vibrations of prey
- Once prey captured, it is injected with a neurotoxin





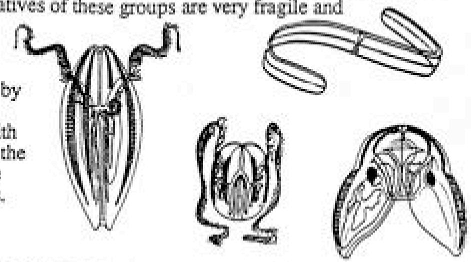
Sagitta euneritica

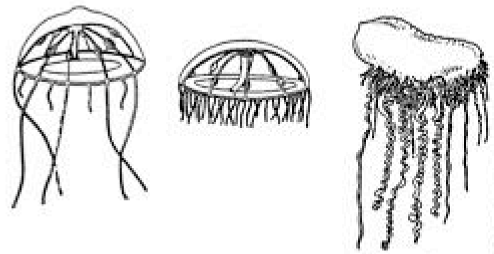
Gelatinous Zooplankton

- Definition based on water content: diverse groups
- *Herbivores*: body adapted to filter large quantities of water (sacks of jelly), e.g., salps, doliolids and appendicularians
- *Carnivores*: sticky tentacles, e.g., tentaculate ctenophores and medusae. Also, lobate ctenophores capture prey using lobed feeding surfaces

GELATINOUS ZOOPLANKTON (Jelly Plankton) - taxonomically diverse grouping sharing a common strategy - high water-content bodies and/or secreted mucus nets increase effective size of animal and its food gathering capability relative to other zooplankton of comparable organic biomass. Many of the oceanic representatives of these groups are very fragile and disintegrate when captured with nets.

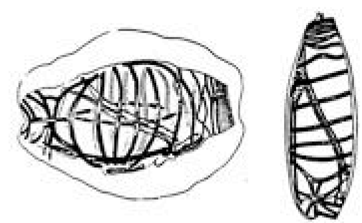
CTENOPHORES - "comb jellies" characterized by bands of joined cilia (comb rows) around body surface. Tentaculate forms have two tentacles with special sticky cells (colloblasts) to entangle prey; the tentacles are "set" like nets. Lobate types capture prey contacting their large lobed feeding surfaces.

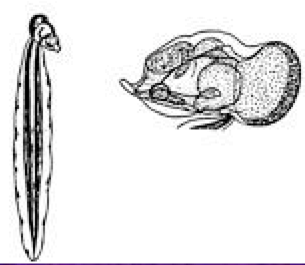




MEDUSAE - Voracious carnivores, food captured by tentacles armed with paralyzing nematocysts. Most coastal (neritic) species alternate generations between attached (benthic) hydroid form which is asexual and a free-swimming, sexual medusae. Most oceanic forms do not have an attached hydroid generation. Siphonophores, the order containing the Portugese man-of-war (*Physalia*), is partiuarly significant in oceanic waters. In these pelagic hydroids, several types of "individuals" perform different "jobs" within the colony.

SALPS - barrel-shaped animal with muscle bands that contract to force water into a buccal opening and out of an atrial opening (jet-propulsion). Ciliary-mucus, filter-feeders - particles in the water current entering the buccal opening are captured on a net of mucus strands which is continuously being passed backward along the gill bar to the esophagus for ingestion. Alternation of sexual (colonies) and asexual (solitary) generations. Salps are chiefly oceanic; dense coastal plankton may clog their feeding mechanism. High food gathering and reproductive capability, sometimes occur in dense swarms.





APPENDICULARIANS (LARVACEANS) - mature forms retain appearance of tadpole chordate larvae, head with tail. Body enclosed in feeding "house". Undulations of tail cause water to enter house through coarse filter where fine particles are concentrated and conveyed to pharynx (mouth?) by a complex collection apparatus (not a simple net). The house is abandoned periodically (predator disturbance or clogged filter) and a new house is built. Old larvacean houses are an important component of "marine snow" in some areas.

Fish

- **Role of fish eggs, larvae and juveniles in open ocean food webs: prey and predator, depending upon life cycle stage**

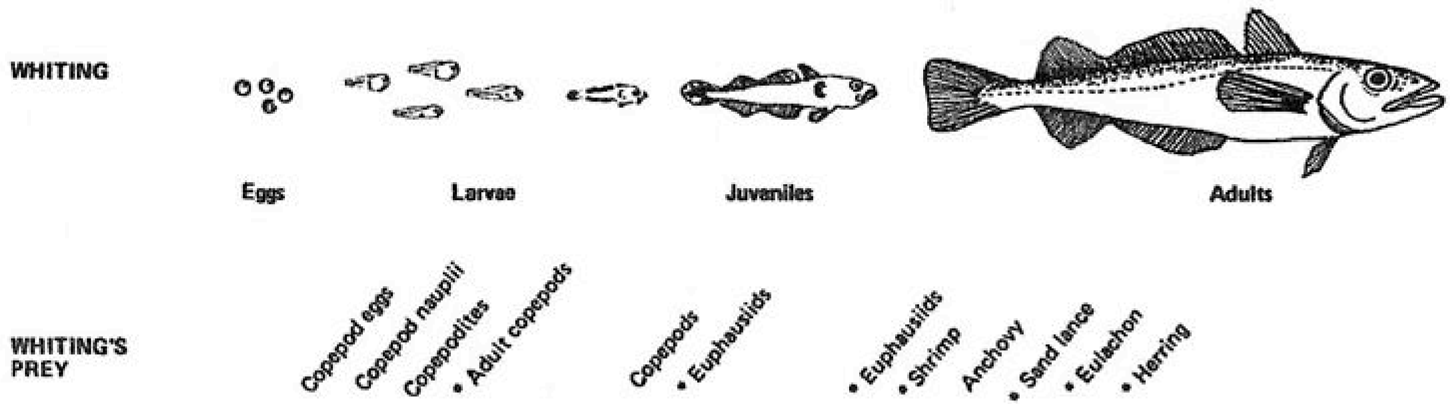


Figure 6.11. Pacific whiting prey fish eaten at various life history stages. (Asterisk indicates major prey species.) Modified from Livingston and Bailey (1985). Mar. Fish. Rev. 42(2):16–22.

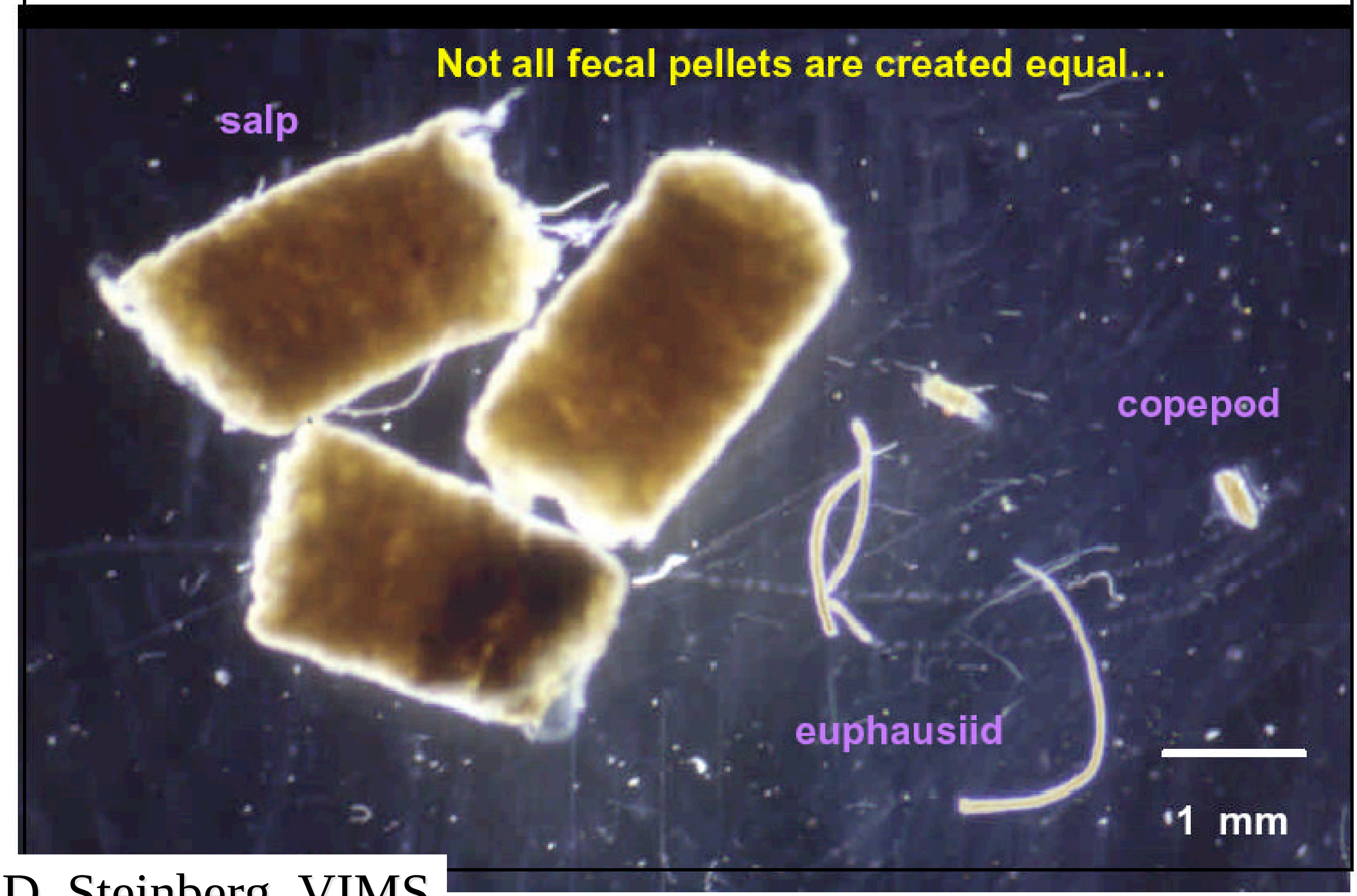
Why should we care that ecosystems differ?

- ***Oceans: an important global sink for CO_2***
  - Surface ocean gases are in equilibrium with atmosphere
  - **Photosynthesis** reduces dissolved CO_2 in ocean water to organic carbon (thus more CO_2 is drawn into the ocean from the atmosphere)
  - High phytoplankton growth rates means lots of CO_2 is reduced to organic carbon daily
  - But, most phytoplankton biomass turned over on a daily basis -- so most organic carbon converted back to CO_2 via **respiration** by heterotrophic organisms
- *The rates of growth/mortality and the amount of carbon that the ocean sequesters depends upon the structure and function of an ecosystem*

POC Transformations: Organisms and their wastes

- Consumer waste products
  - CO_2 (respiration)
  - Excretion of low MW material (e.g., amino acids, etc.)
  - Egestion of “dissolved” organic matter or particulate organic mater
- Microzooplankton (Protist) Waste
  - POC to DOC or CO_2 - major remineralization role
- Mesozooplankton (Metazoan) Waste
  - POC to DOC or CO_2 - lesser role than protists
  - POC to packaged POC/DOC - vertical flux
  - Vertical Migrants - transport of wastes to deep waters

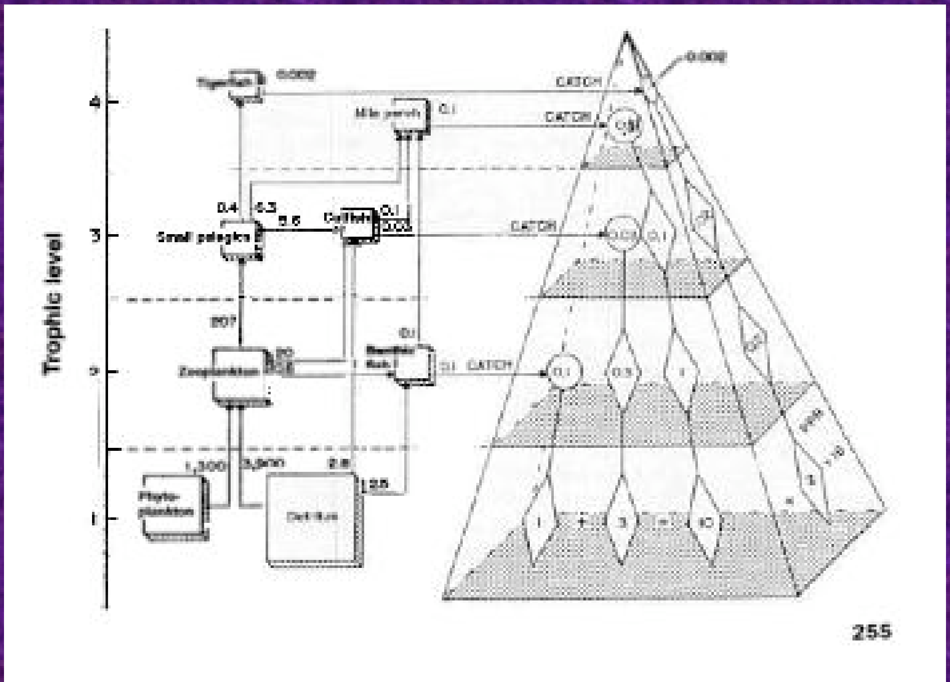
Fecal Pellets



D. Steinberg, VIMS

Yields of Fish from Ecosystems

The structure of ecosystems also governs fish yields, since every step in the food chain reduces the amount of organic carbon available to the next higher trophic level



Pauly & Christensen 1995

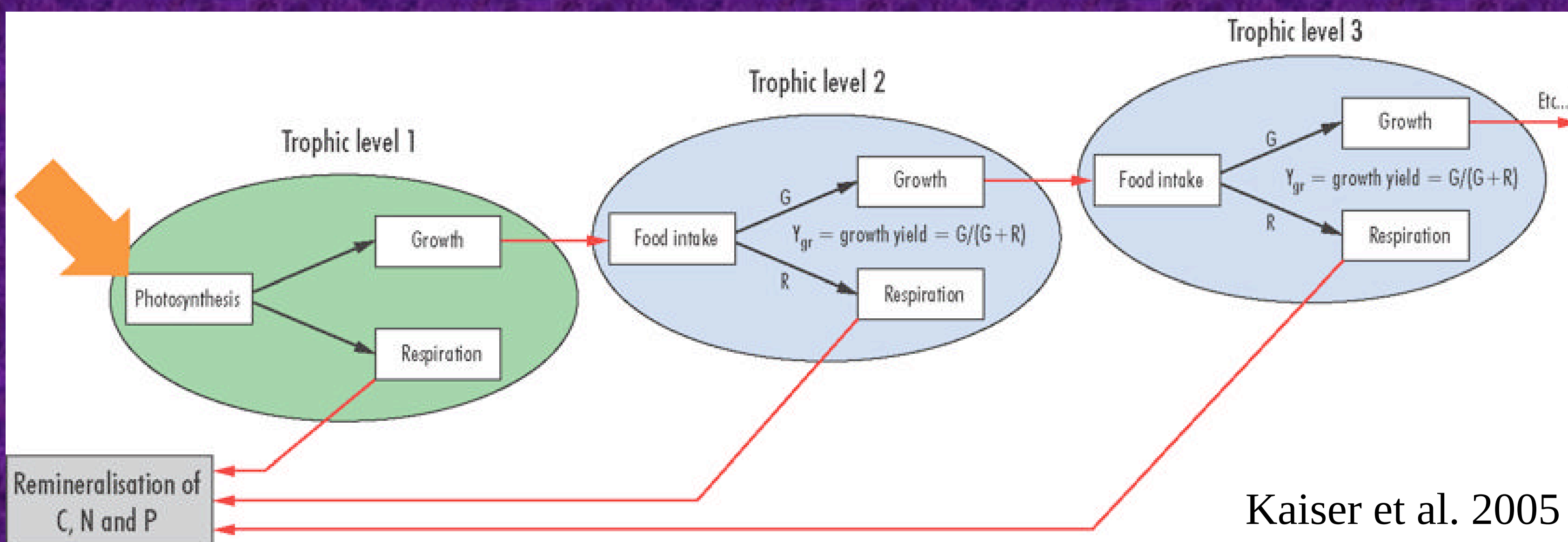
Trophic Transfer Efficiency

TTE (or Trophic Yield) = *Amount of production at trophic level (X+1) relative to production at trophic level X*

Because of losses to metabolism/egestion at each step, longer food chains result in less yield to the top predator

How to apply to actual food chain?

Overall Food Chain Efficiency = TTE(2)*TTE(3)*TTE(4)*TTE(n)



Kaiser et al. 2005

Micro- & Meso-Zooplankton: Feeding

Feeding

- What do feeding rates tell us about marine ecosystems?
  - Death rates of organisms consumed ("top down controls"): mortality rates
  - Transfer of biomass to higher trophic levels
    - implications for ultimate yield of biomass

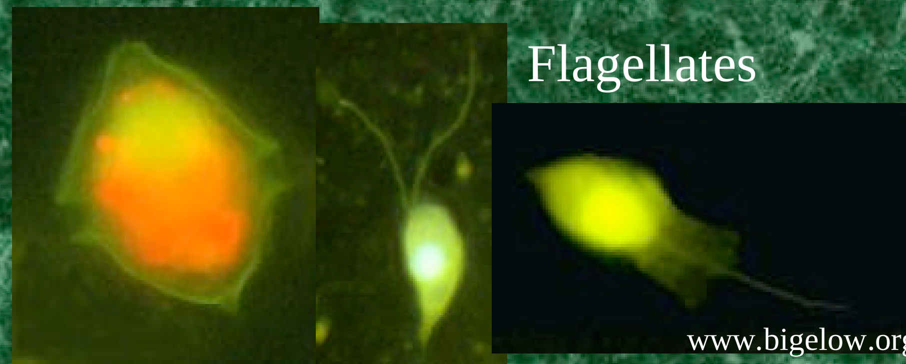
      or
    - downward flux of fixed carbon
  - Implications for nutrient remineralization

Pelagic planktonic consumers: Feeding modes

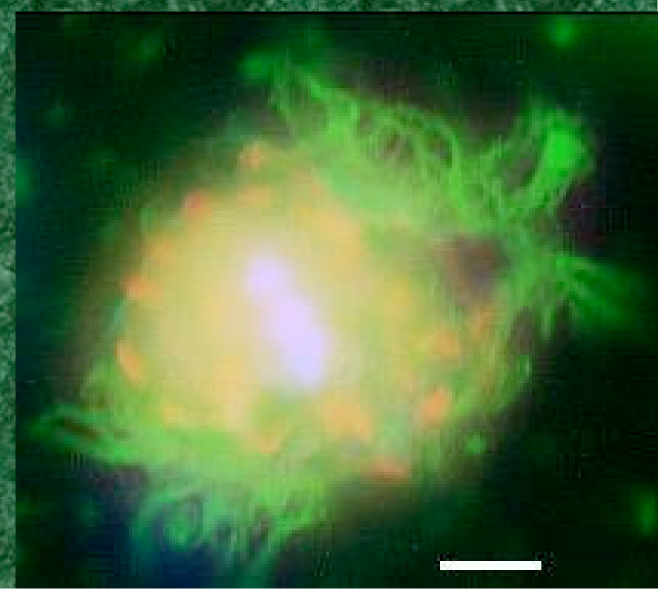
- **Protists:** diffusion feeding, direct interception, filter feeding, dinoflagellate feeding diversity, mixotrophy
- **Crustacea:** filter and raptorial feeding
- **Chaetognaths**: raptorial feeding (ambush predators)
- **Gelatinous Zooplankton**: tentacles, sticky cells and filter feeders
- **Larval Fish**: mainly raptorial feeders, although some notable groups do filter feed

Microzooplankton: single-celled eukaryotes (just like many phytoplankton)

Ciliates



Flagellates



Heterotrophic - Consume particulate food (bacteria/phytoplankton/other microzooplankton)

Can be **Mixotrophic** -- Consume particulate food and function as an autotroph

Who do they feed on?
Regional Comparisons of Microzooplankton Grazing Impact

60 - 75% of daily production consumed by microzooplankton

Table 1. Regional comparisons of system characteristics from dilution experiments. Data are distinguished among *Oceanic*, *Coastal* (overlying the continental shelf), and *Estuarine* (including coastal bays) habitats in the upper table and among *Tropical/Subtropical*, *Temperate/Sub-polar*, and *Polar* regions in the lower table. Mean values (± standard errors) are given for initial Chl *a*, phytoplankton growth rate (μ), grazing mortality (m), and percentage primary production grazed d^{-1}. Exp = number of experimental estimates averaged for the region, out of a total of 788.

	Exp (% total)	Chl *a* ($\mu g\ l^{-1}$)	μ (d^{-1})	m (d^{-1})	% PP grazed
Oceanic	510 (65%)	0.58 ± 0.03	0.59 ± 0.02	0.39 ± 0.01	69.6 ± 1.5
Coastal	142 (18%)	3.06 ± 0.53	0.67 ± 0.05	0.40 ± 0.04	59.9 ± 3.3
Estuarine	136 (17%)	13.0 ± 1.8	0.97 ± 0.07	0.53 ± 0.04	59.7 ± 2.7
Tropical	259 (33%)	1.01 ± 0.21	0.72 ± 0.02	0.50 ± 0.02	74.5 ± 2.0
Temperate	435 (55%)	5.18 ± 0.66	0.69 ± 0.03	0.41 ± 0.02	60.8 ± 1.8
Polar	94 (12%)	0.62 ± 0.06	0.44 ± 0.05	0.16 ± 0.01	59.2 ± 3.3

Landry & Calbet 2004, Microplankton production in the oceans, ICES J. of Mar. Science 61:501-507

Food Vacuoles

Intracellular vacuoles digest the food (no gut as in metazoans)

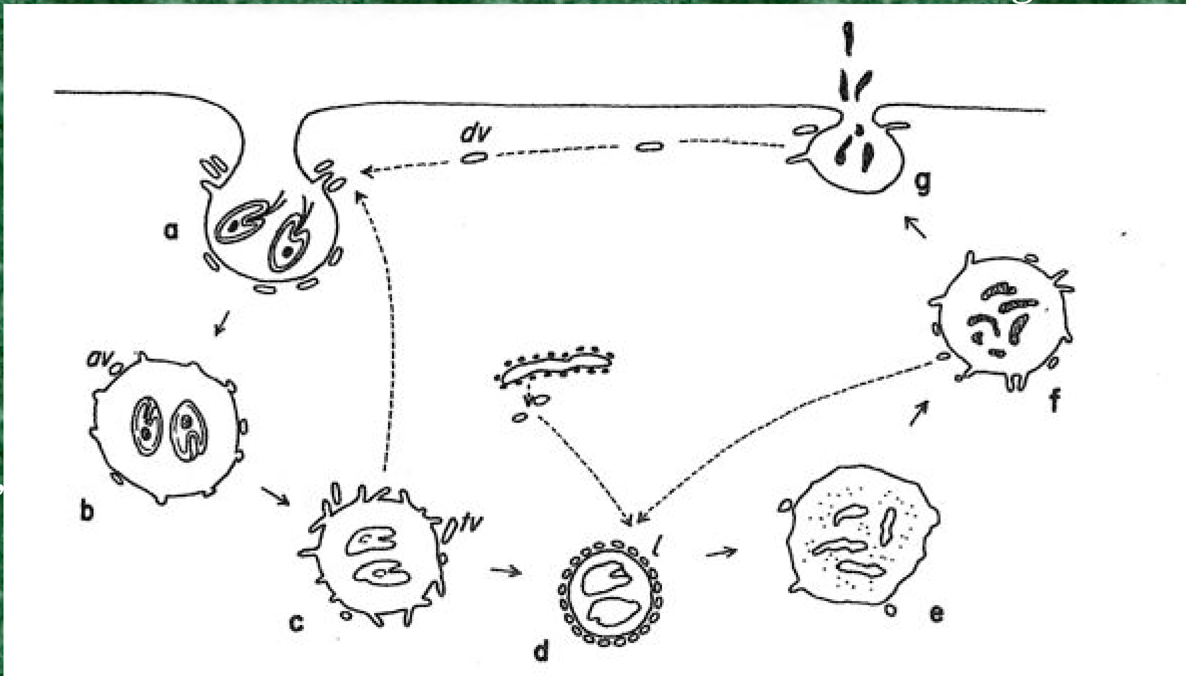
Example of a food vacuole cycle in a protist:

Sleigh 1989

a: food vacuole "pinching off" from outer membrane, enclosing food items (phagocytosis)

b: it fuses with acid-containing vesicles (av)

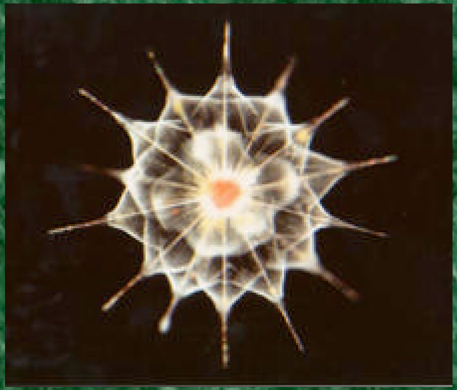
c & d: it shrinks as liquid is removed, then merges with lytic (lysosomal) enzymes (digestion)



e & f: after food digestion, digested vacuolar contents are pinched off into cytoplasm, as are the enzymes for re-use

g: undigested material may be released to the "outside" environment (remineralization) and the membrane retrieved to be re-used for another cycle

Microzooplankton Feeding Modes



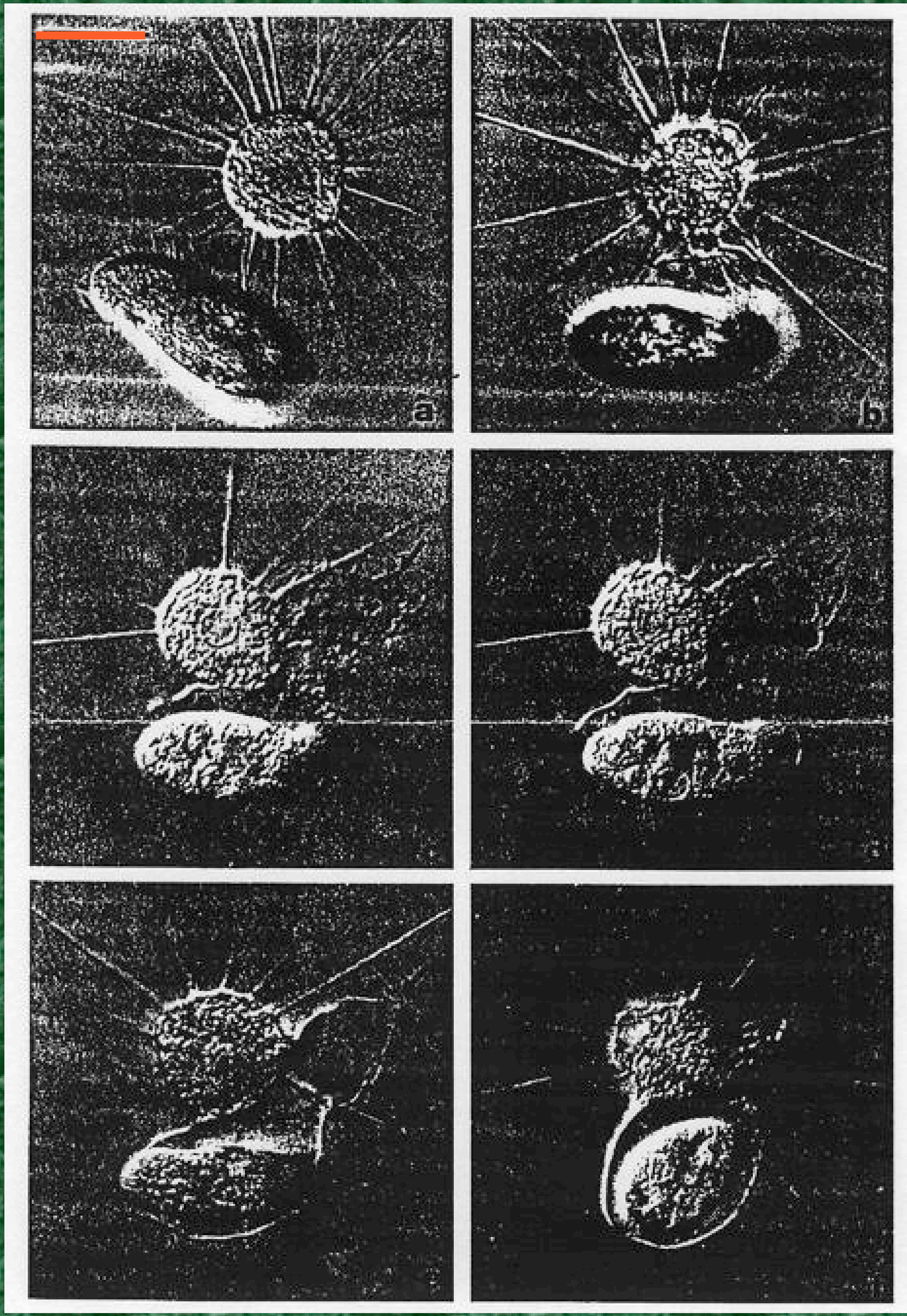


- Sarcodines: Diffusion feeding (except amoebae)
- Flagellates: Direct interception
- Ciliates, some flagellates: Filter (suspension) feeding
- Dinoflagellates: peduncle and pallium feeding

Protist Motility: pseudopods

- Sarcodines: e.g., amoebae

http://www.isengrim.com/lasaterd43.html



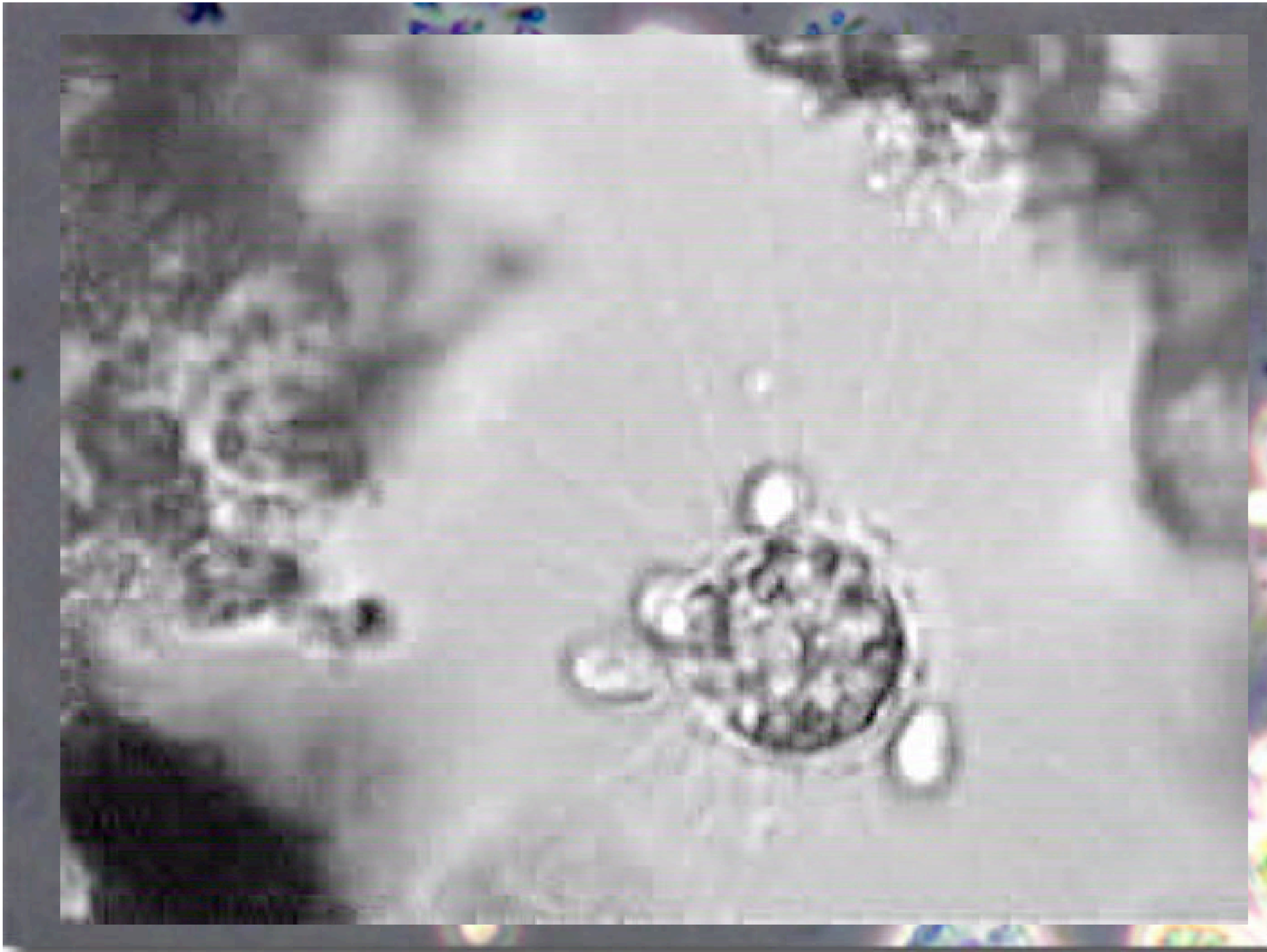
Diffusion Feeding

Actinophry sol (heliozoan) capturing the ciliate *Colpidium*.

a) adhesion
b) pseudopod extension
c/d) pseudopod wrapping around prey
e/f) prey completely enclosed

scale bar = 50 µm

Hausmann & Patterson 1982



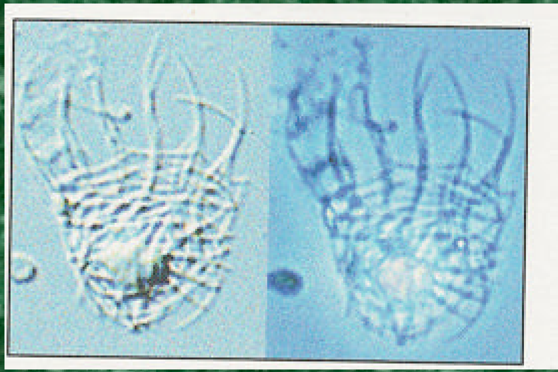
Direct Interception Feeding

- Performed by the smallest protists (flagellates)
- The most important grazers of bacteria ("bacterivory"), but also feed on smaller algae
- Ubiquitous and abundant in aquatic ecosystems

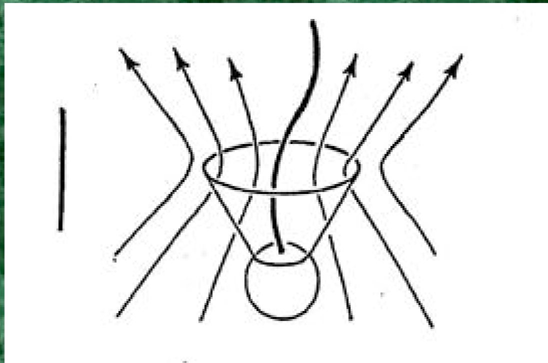
Images courtesy of Bay Paul Center http://starcentral.mbl.edu/microscope/portal.php,

Filter feeding - choanoflagellates

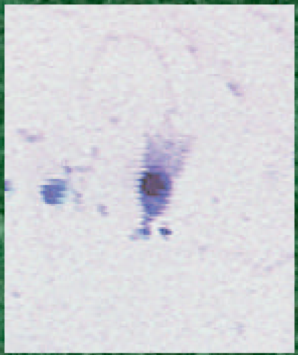
*most important bacterivores in the Southern Ocean



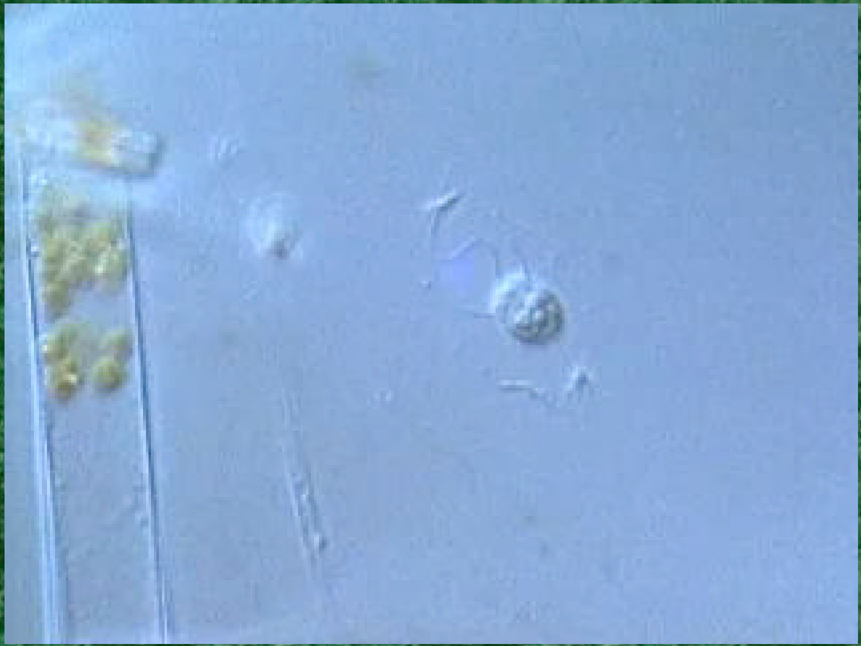
Acanthocorbis unguiculata (dry prep)



Fenchel 1986



Parvicorbicula quadricostata
(Southern Ocean)



http://www.aad.gov.au/

Ciliate filter feeding

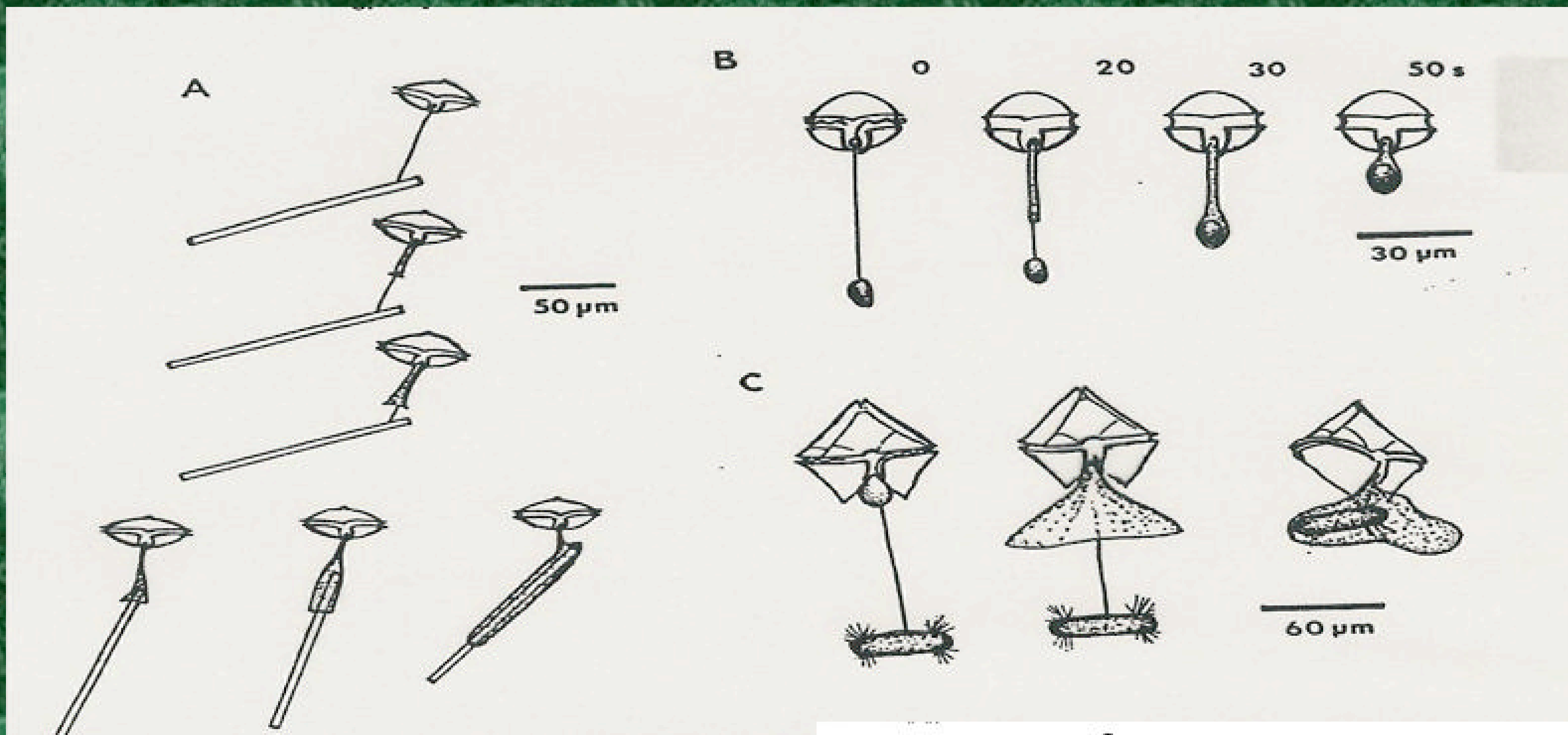
*feed on bacteria, but usually more important as predators of eukaryotic phytoplankton

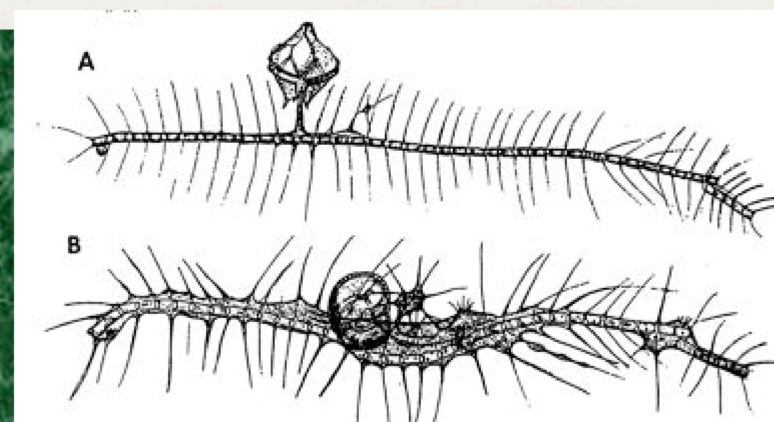
http://www.aad.gov.au/

Video by Harvey Marchant

http://www.aad.gov.au/

Pallium Feeding by Dinoflagellates*





**Most important consumers of diatoms amongst the microzooplankton*

figures from Jacobsen & Anderson 1986

Gymnodinium feeding

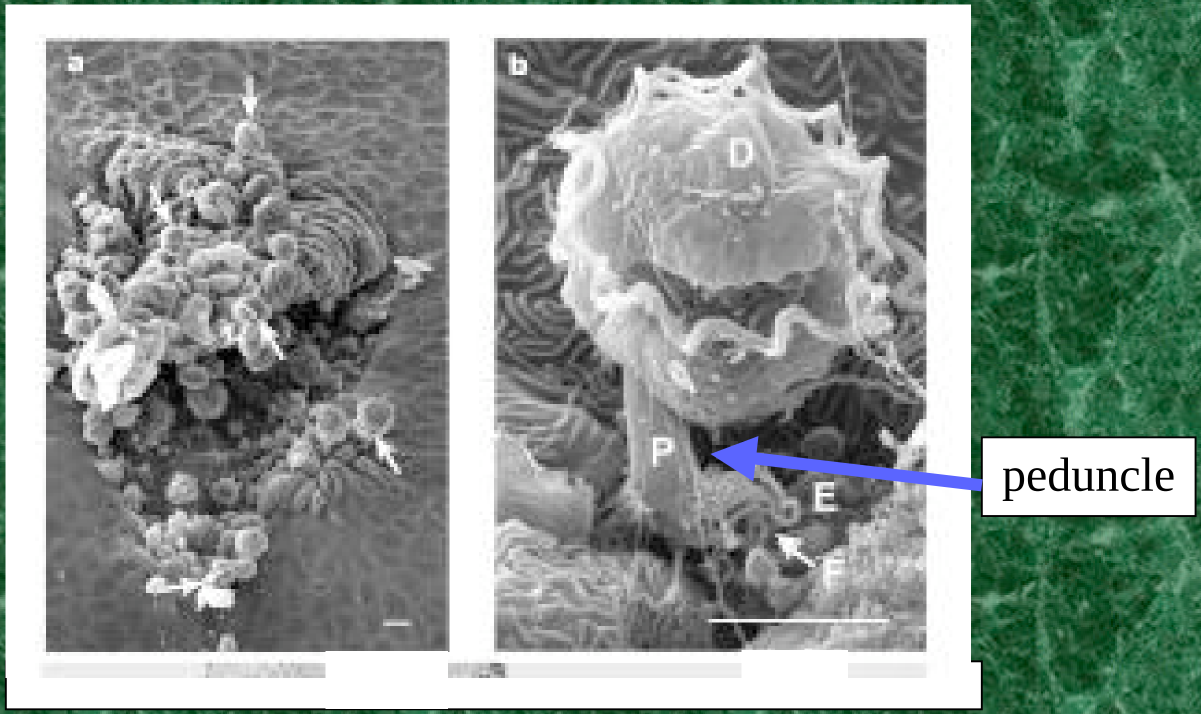
- Peduncle feeding of *Gymnodinium fungiforme* extending into unidentified food particle

  (Spero & Spero 1982)

Peduncle Feeding by Dinoflagellates (Myzocytosis)

e.g., Pfiesteria spp.: fish killed by dinoflagellate predation

A larval sheepshead minnow (*Cyprinodon*) being fed upon by *Pfiesteria*



fish skin lesion w/dinos attached

Vogelbein et al. 2002

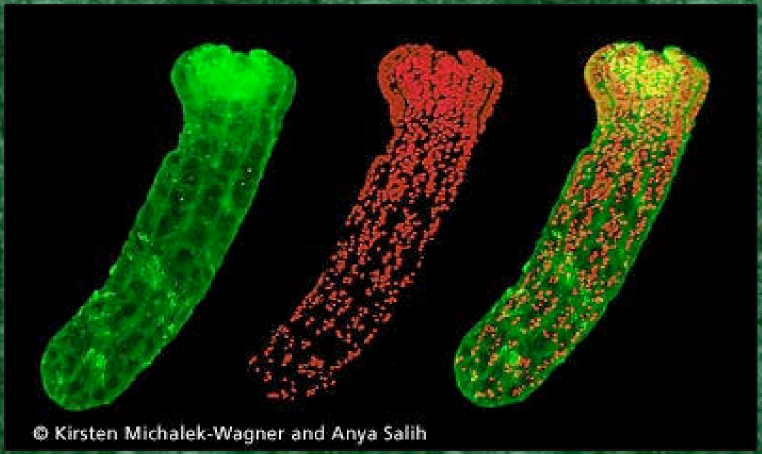
Mixotrophy

- Mixed mode of nutrition, definition broad enough to include symbiotic relationships
- Widespread amongst protistan groups
- Diverse: manifests in many ways

Advantages & Functions of Mixotrophy

- ✎ Gas exchange--oxygenation of large cells
- ✎ Source of nutrients/organics for basically autotrophic cell in an oligotrophic environment
- ✎ Protection, advantage to symbionts

For corals, symbionts supply the added nutrition required for secretion of $CaCO_3$ skeletons



http://www.reefed.edu.au/home/explorer/plants/

Three General Types of Mixotrophy

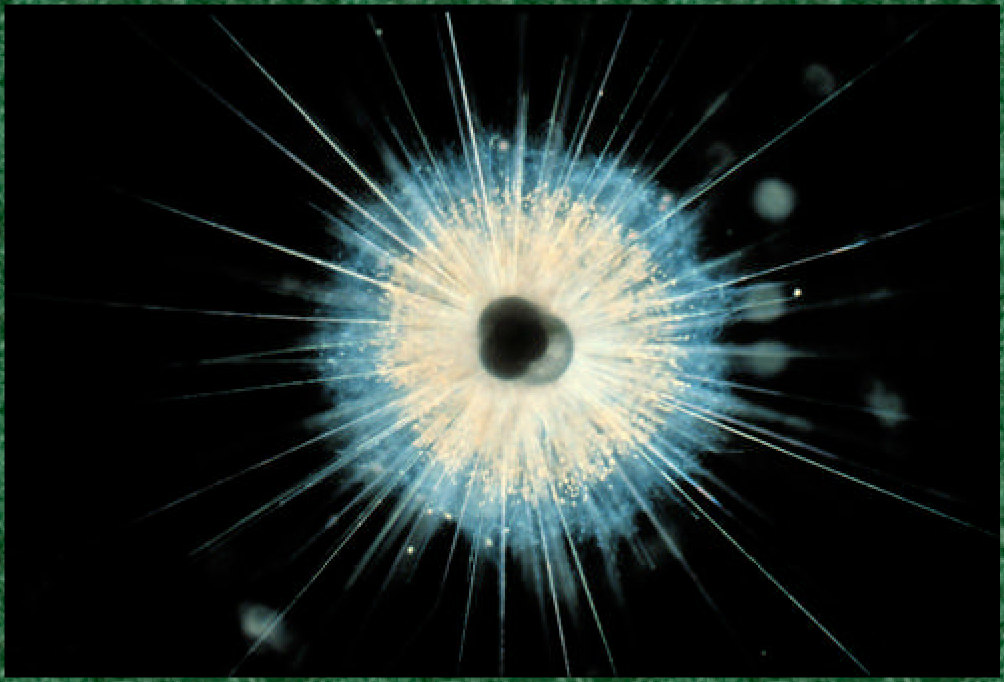
1. Endosymbiotic relationships: true symbiotic relationships, like algae in corals

• *mostly associated with Sarcodines -- symbionts are often dinoflagellates, monads, diatoms, red algae*

• *usually only one symbiont type per host species*

• *enclosed in vacuolar membrane, "respectful distance"*

Globigerinoides ruber
with dinoflagellate symbionts



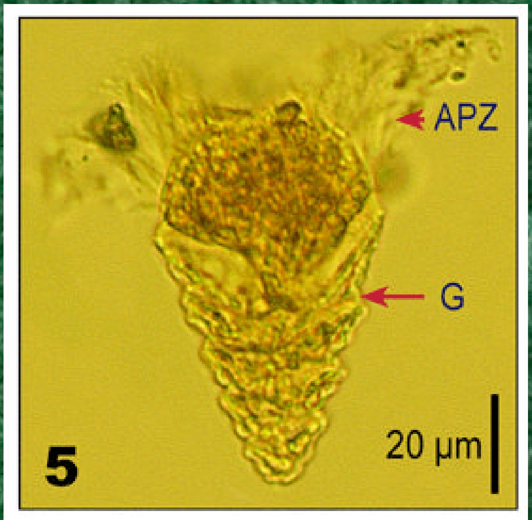
2 mm

image courtesy of D. Lea, UCSB

2. Borrowed chloroplasts

Example: Laboea strobila, a tintinnid ciliate, borrows chloroplasts, it may eat some at night -- gets mainly polysaccharide sugars and LMW molecules from chloroplasts

- Implication: since “prey” may continue to produce organics for predator after ingestion, efficiency of growth might be higher than predicted simply from ingestion of prey biomass

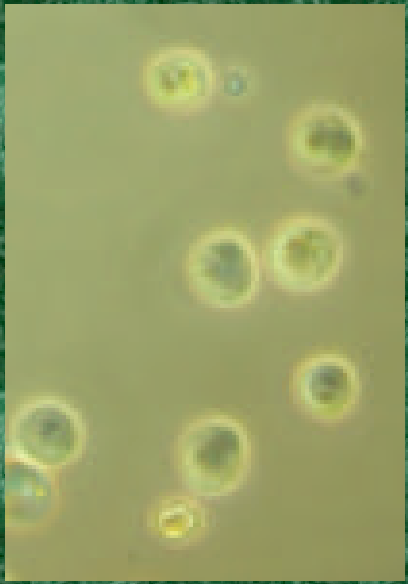


http://www.liv.ac.uk/ciliate

3. Inherent part of Organism's Structure (genome)

Example: Mixotrophic flagellate (chrysophyte) P. malhamensis, phagotrophy dominates if bacteria are present, phototrophy only when bacterial abundance becomes limiting.

- Other organisms may show the opposite preference for trophic mode.



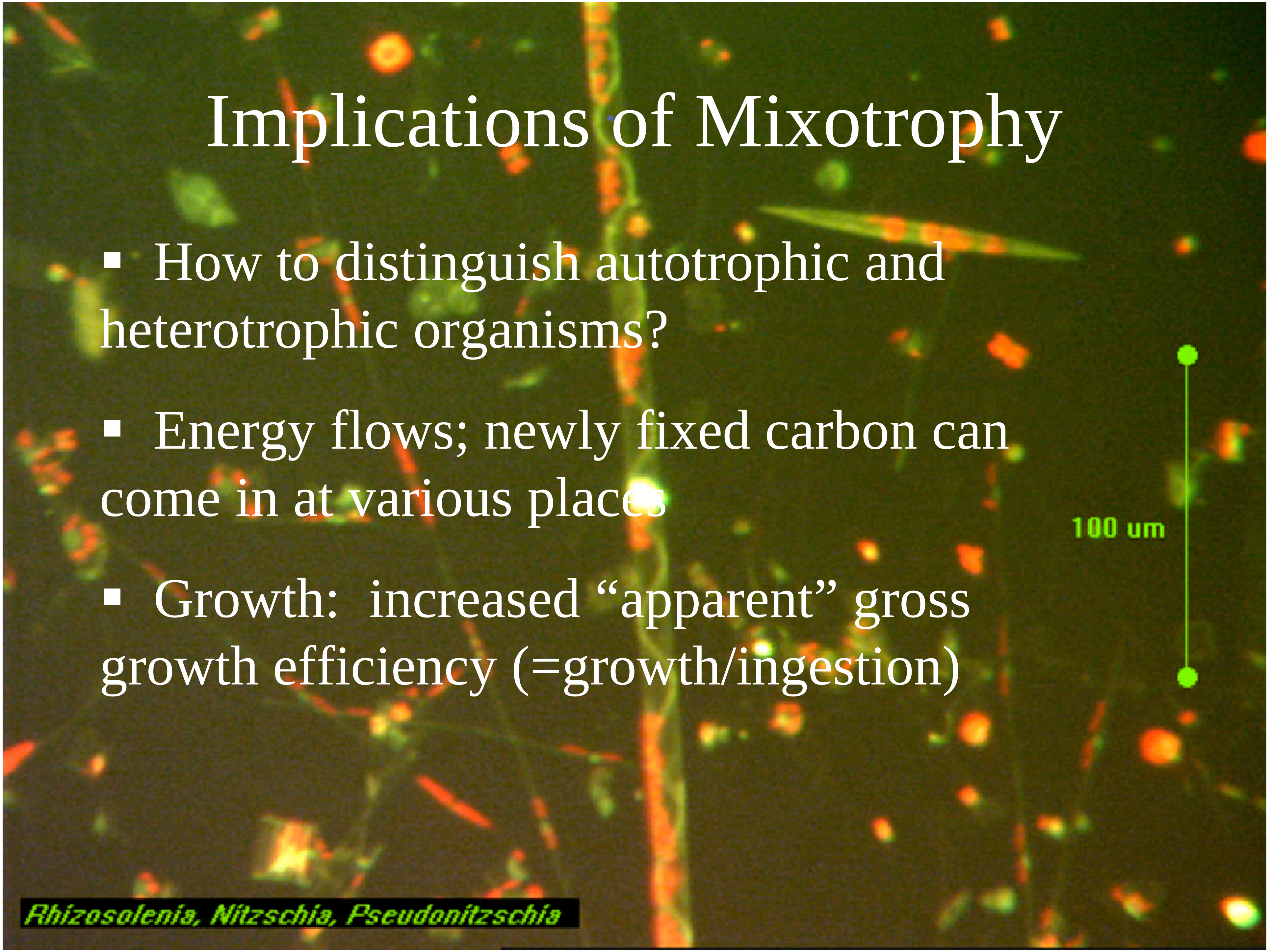
Carina Pålsson
www.limnol.lu.se/limnologen

Prorocentrum minimum

www.sb-roscoff.fr/Phyto/gallery/

Implications of Mixotrophy

- How to distinguish autotrophic and heterotrophic organisms?
- Energy flows; newly fixed carbon can come in at various places
- Growth: increased "apparent" gross growth efficiency (=growth/ingestion)



Summary of Feeding Modes

Feeding mechanisms: 4 main types

- *Filter or suspension feeding*
- *Diffusion feeding*
- *Pallium and peduncle feeding*
- *Direct interception (raptorial) feeding*

Mixotrophy: 3 main types

- *Endosymbiosis (true partnership)*
- *Kleptochloroplasts (“borrowed” chloroplasts)*
- *Genetically capable of switching (“autonomous” mixotrophs)*