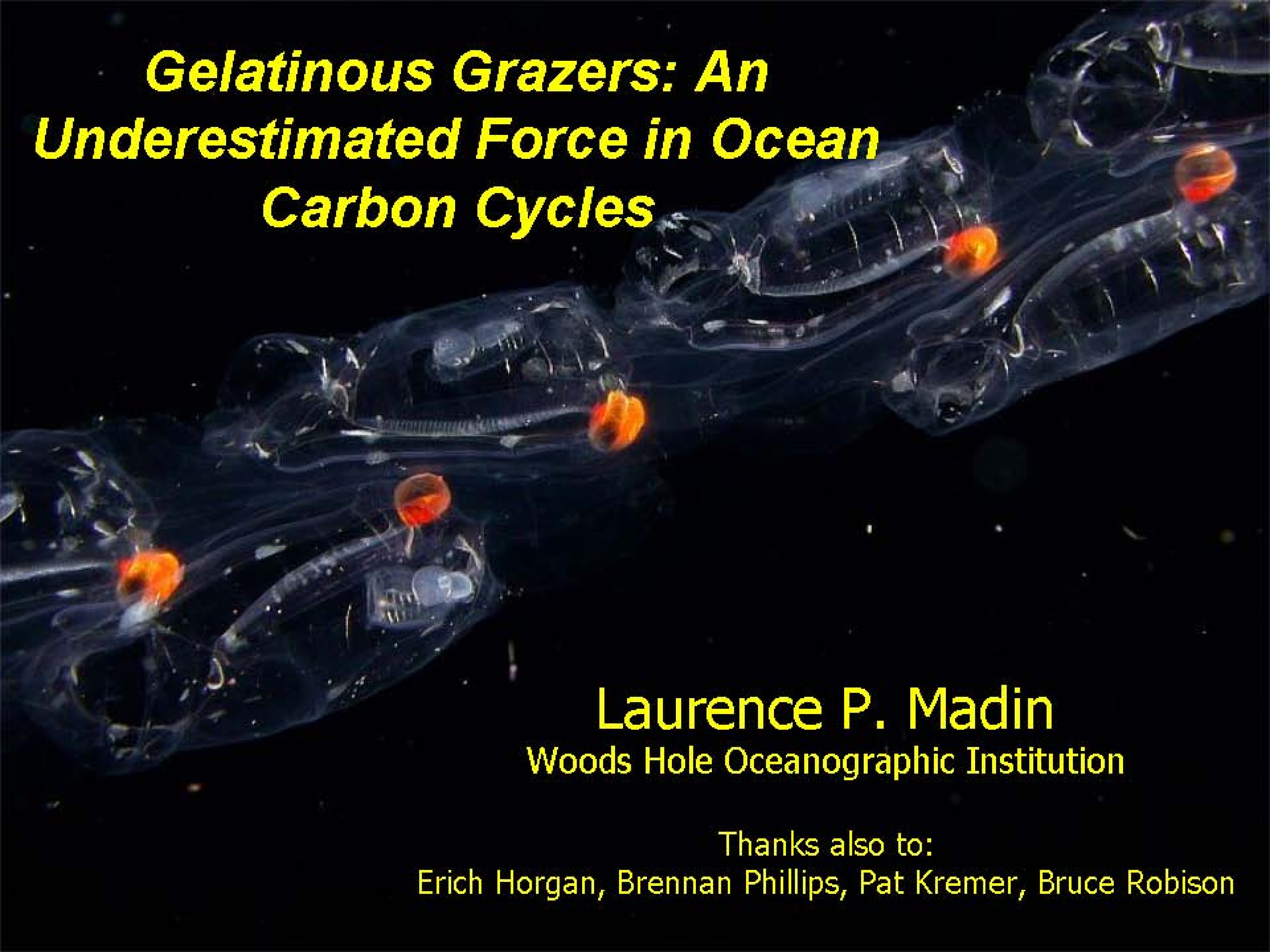
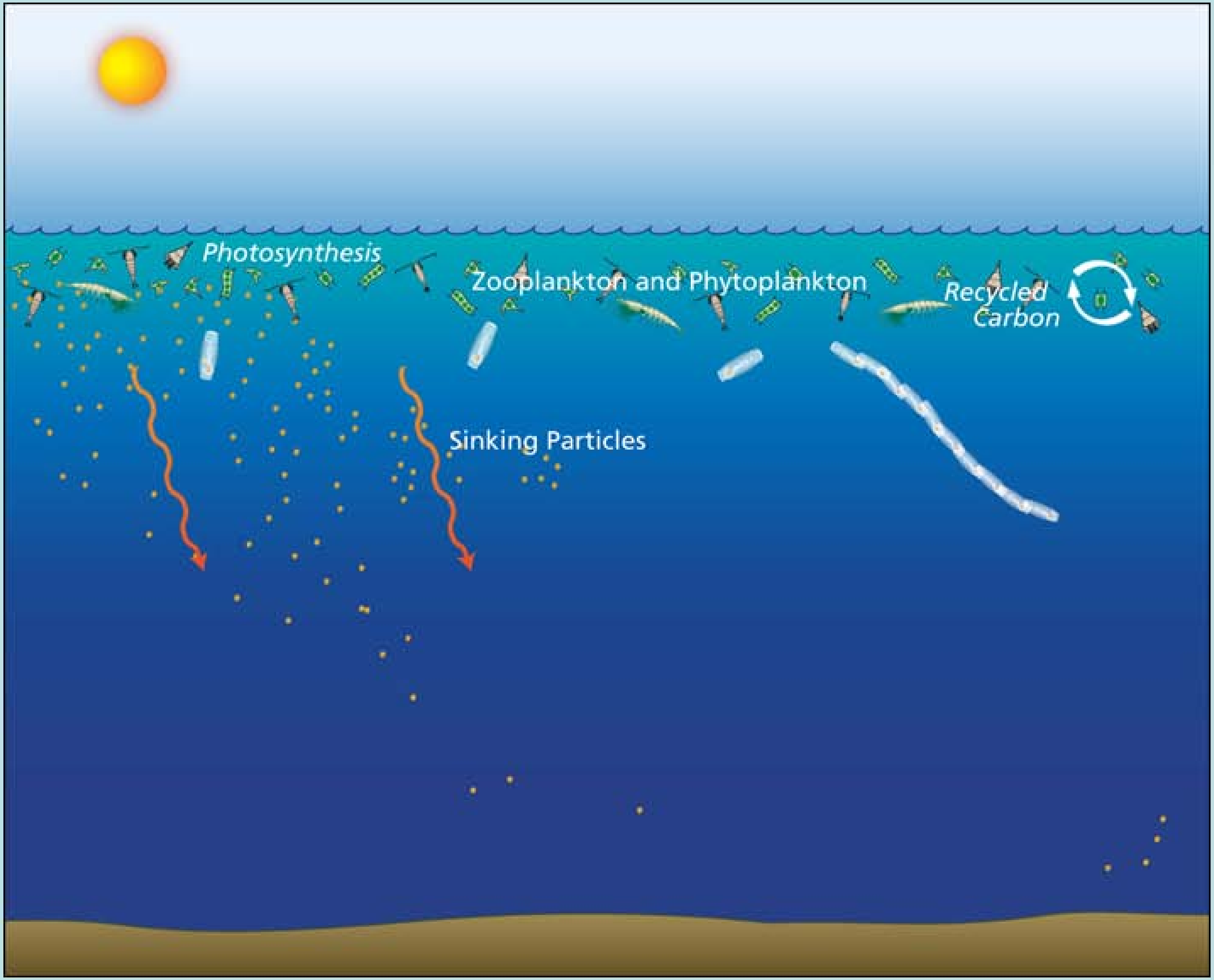


Gelatinous Grazers: An Underestimated Force in Ocean Carbon Cycles

Laurence P. Madin
Woods Hole Oceanographic Institution

Thanks also to:
Erich Horgan, Brennan Phillips, Pat Kremer, Bruce Robison

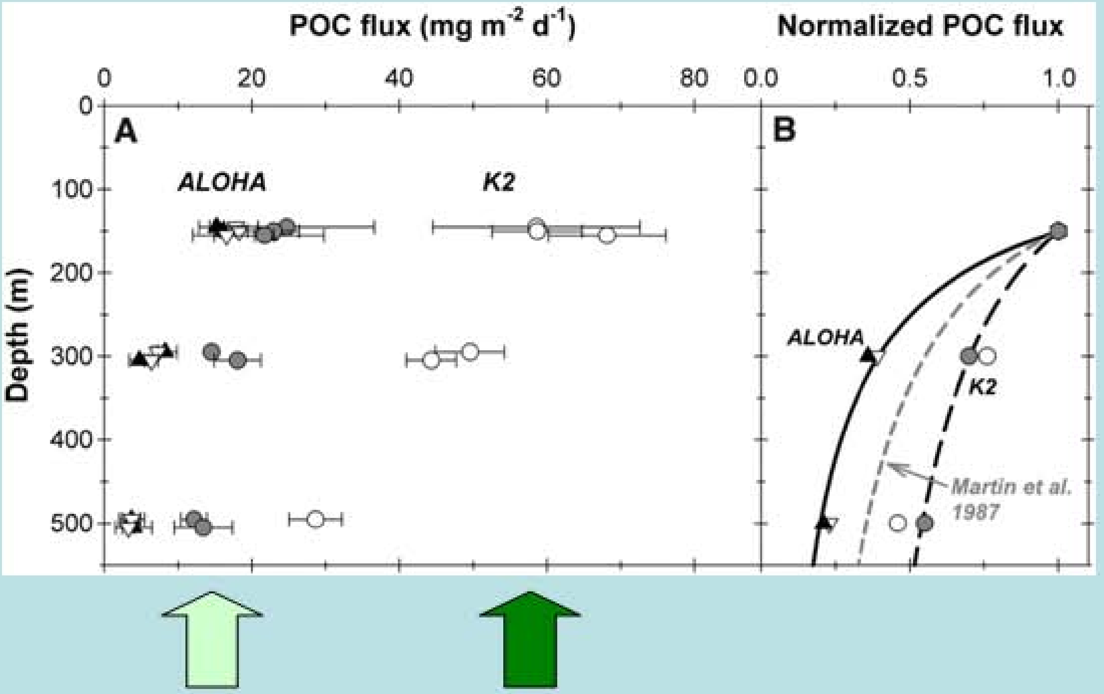
The Biological Pump



Downward flux due to sinking cells, detritus, fecal pellets, carcasses, or via diel migration

Recycling vs sinking depends on type and size of particles and nature of metabolic activity

Variability in C Flux



Hawaii North Pacific

General parameters affecting C flux rate

- Primary production rate
- Particle size, density (cells vs pellets)
- particle aggregation, marine snow formation
- Water temperature, stratification
- Grazer composition, abundance & behavior
- Secondary consumption, degradation

Buesseler et al. 2007

Community composition affects export

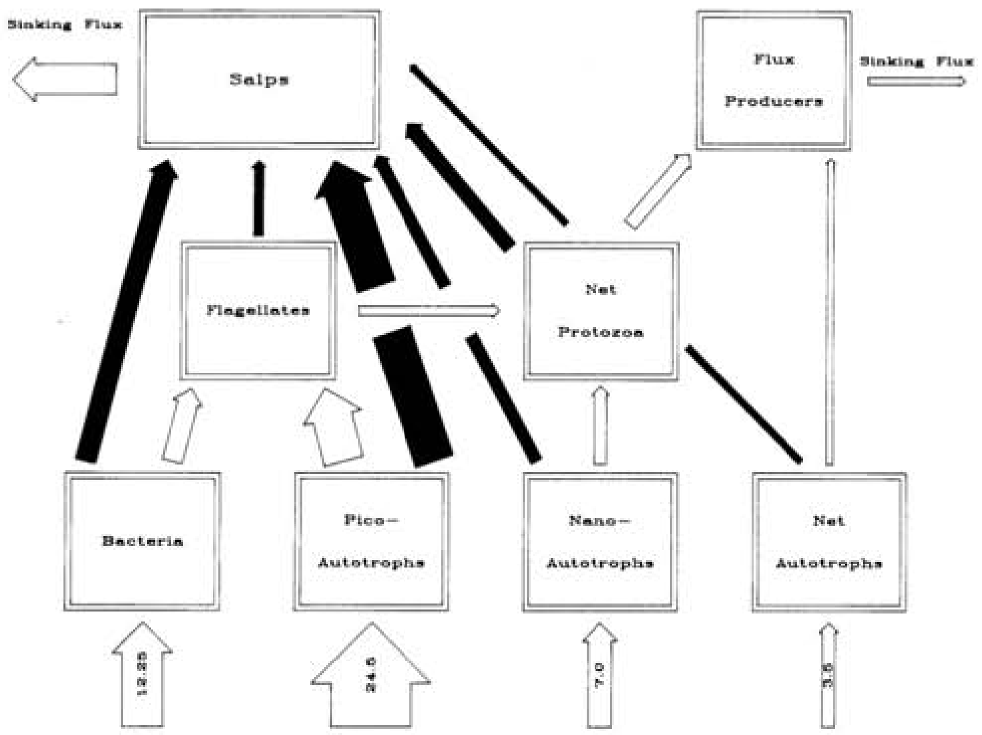


Fig. 4. The salp food web. A modification of the basic web, which adds a new grazer, typified by salps, that can ingest food from the entire size range of organisms. The widths of the arrows are in proportion to the flows for the 50% salp food web.

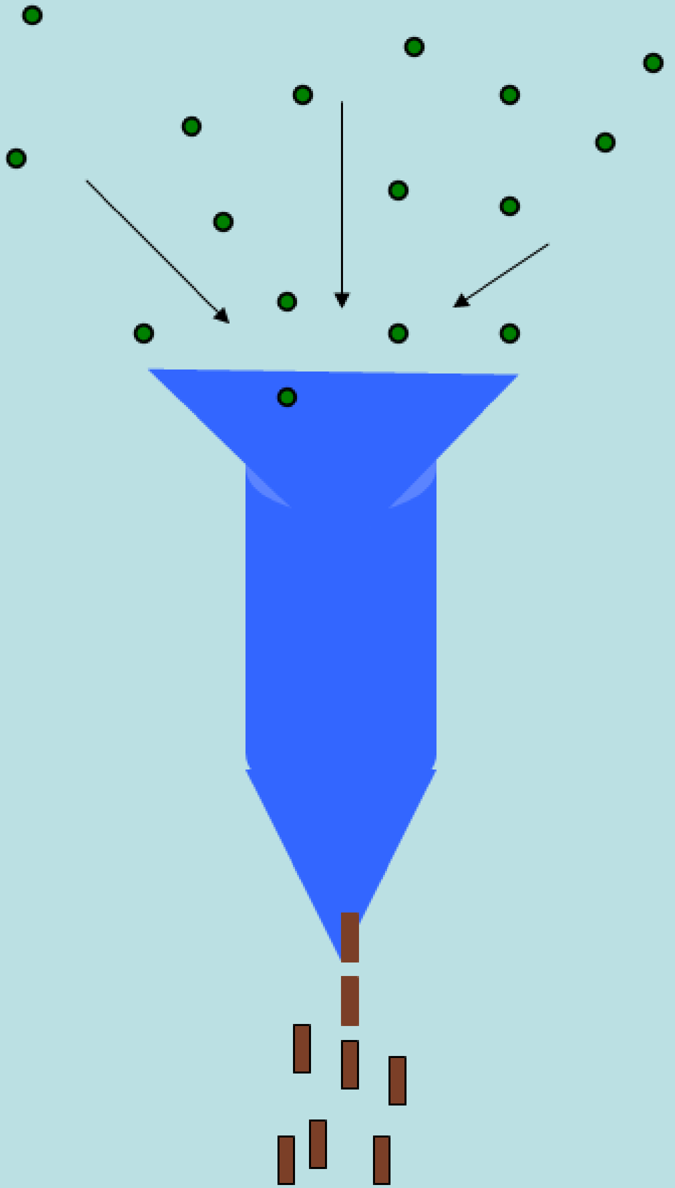
Comparison of theoretical plankton communities:

- significant export required presence of 'generalist grazers' like salps
- export of picoplankton may rely on salp feeding
- salps & doliolids in California Current could account for 22% of N export
- patchy occurrence and variable abundance makes role hard to sample or predict

Michaels & Silver 1988

Richardson & Jackson 2007

The Ideal Carbon Fluxer

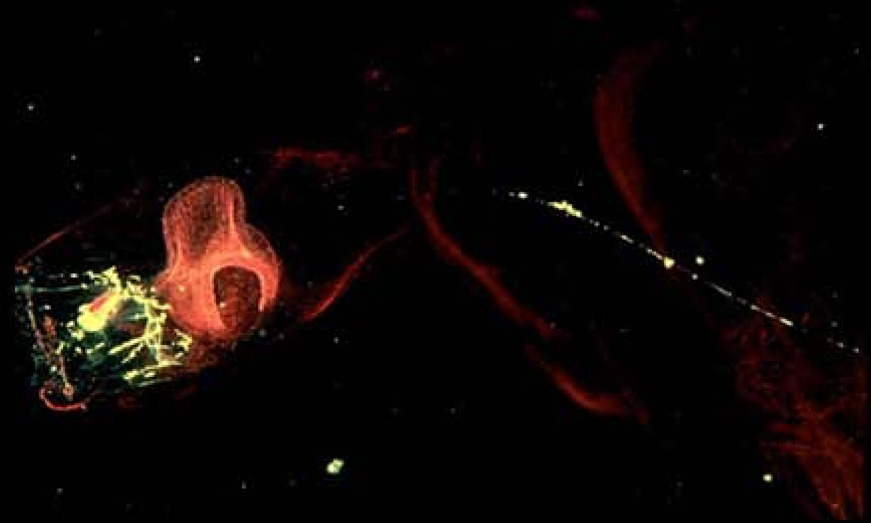


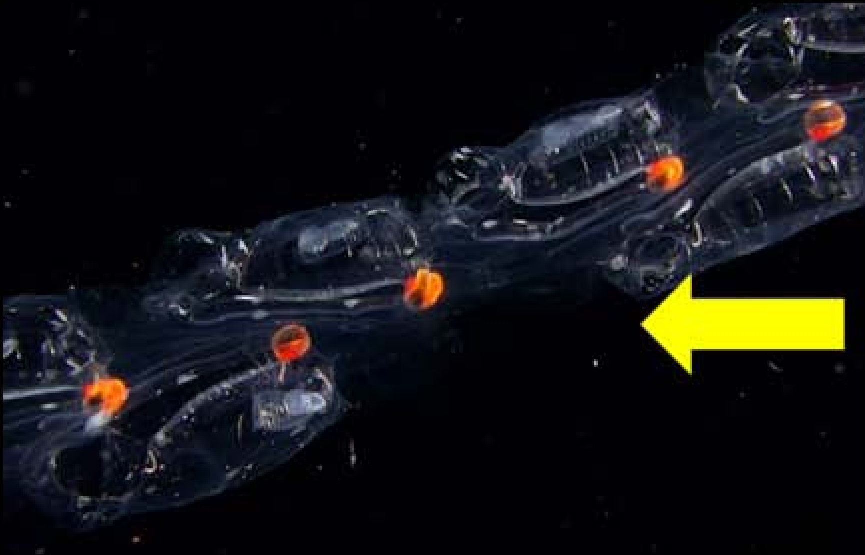
Grazers:

- High rates of grazing and defecation
- Broad particle size and type selection
- Large population sizes
- Broad geographical distributions
- Rapid population response to production
- Diel vertical migration
- Sinking carcasses

Fecal Pellets:

- Large and dense
- High sinking rates
- Resistant to degradation





Salps

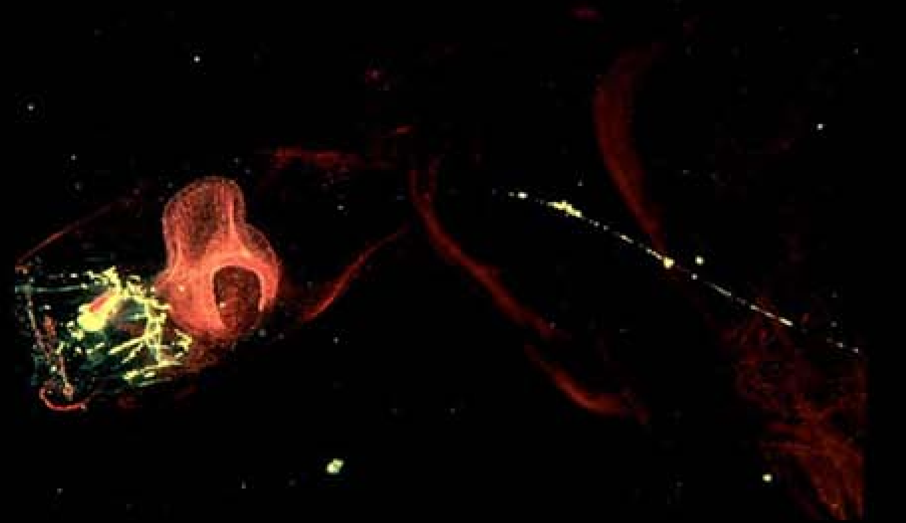
Size: individuals 1 to 30 cm, chains to 4 m

Reproduction: alternating sexual & asexual stages, hermaphroditic, high fecundity, fertilization & survival, no larval stages

Generation time: weeks to months

Colony: isomorphic individuals, limited integration, varying chain shapes

Growth rates: high to moderate



Pyrosomes

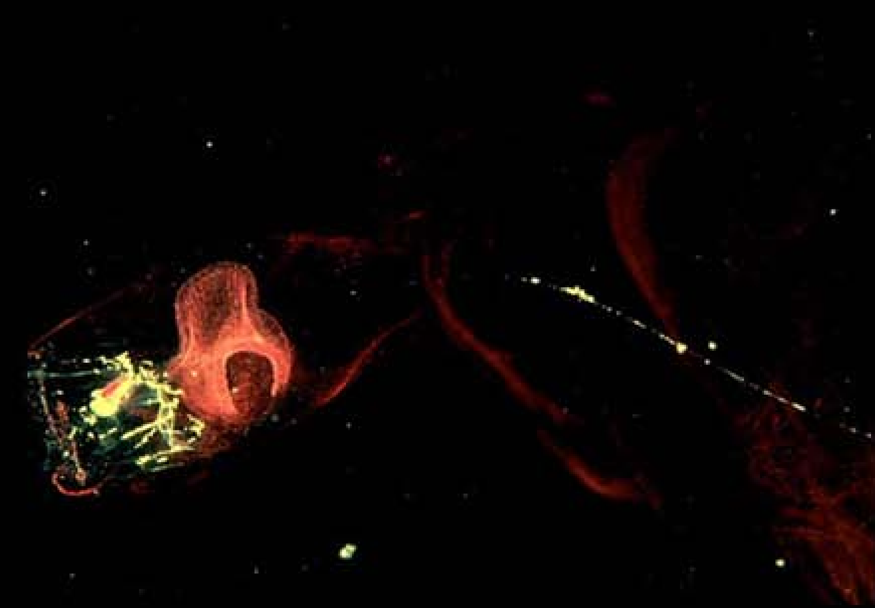
Size: individuals to 1 cm, colonies to 20 m

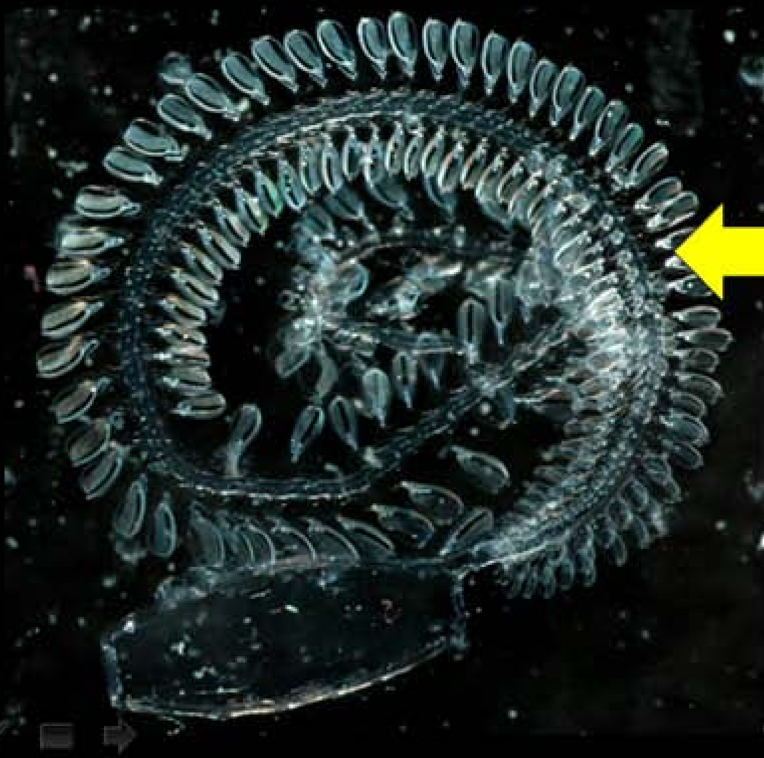
Reproduction: sexual & asexual modes, hermaphroditic, no larval stage

Generation time: unknown

Colony: isomorphic individuals in rigid or flexible hollow tubular colony

Growth rates: unknown





Doliolids

Size: individuals ≤ 5 cm, colonies to 2 m

Reproduction: 1 sexual & multiple asexual stages, hermaphroditic, high fecundity, some larval stages

Generation time: weeks ?

Colony: polymorphic individuals, complex integration, varying shapes

Growth rates: high to moderate

Appendicularians

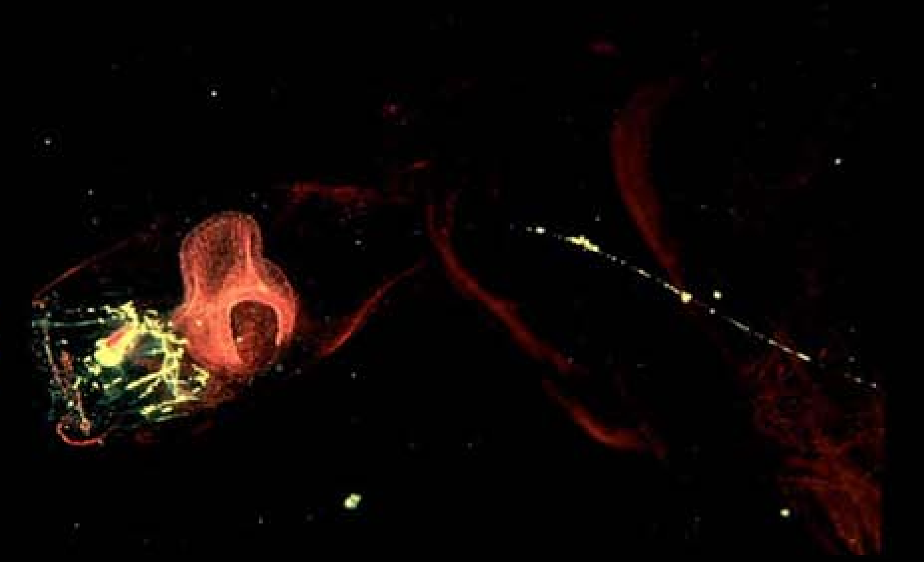
Size: individuals ≤ 1 cm

Reproduction: sexual, hermaphroditic, no larval stages

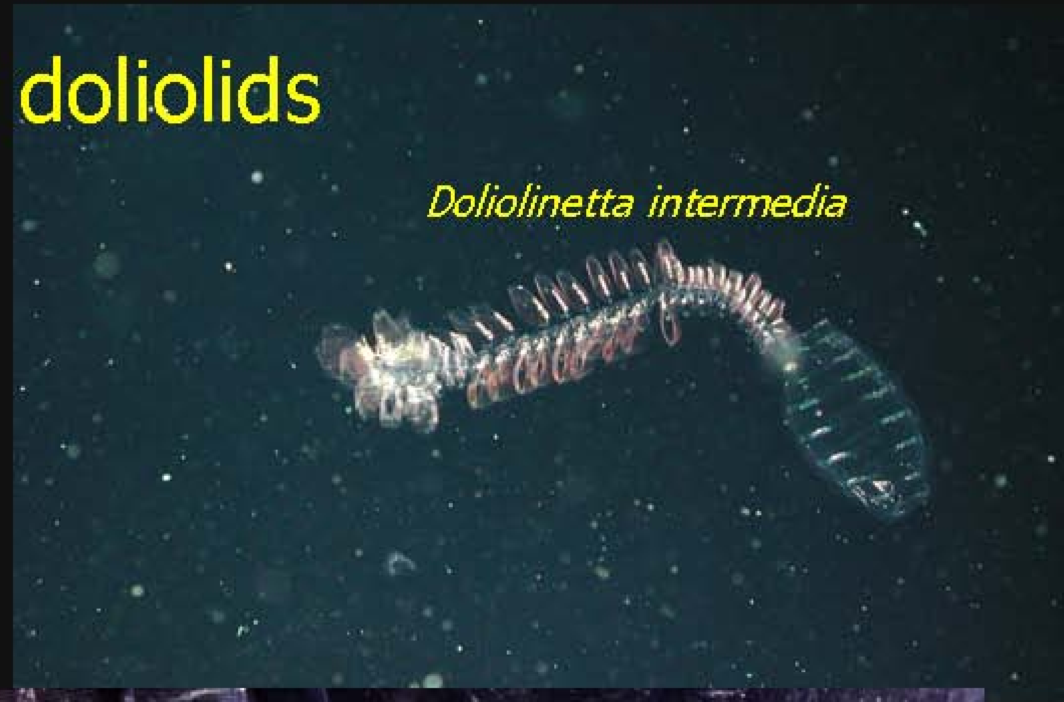
Generation time: days

Colony: none

Growth rates: very high



Midwater salps and doliolids




Another underestimated
source of C flux

Tunicate grazing characteristics

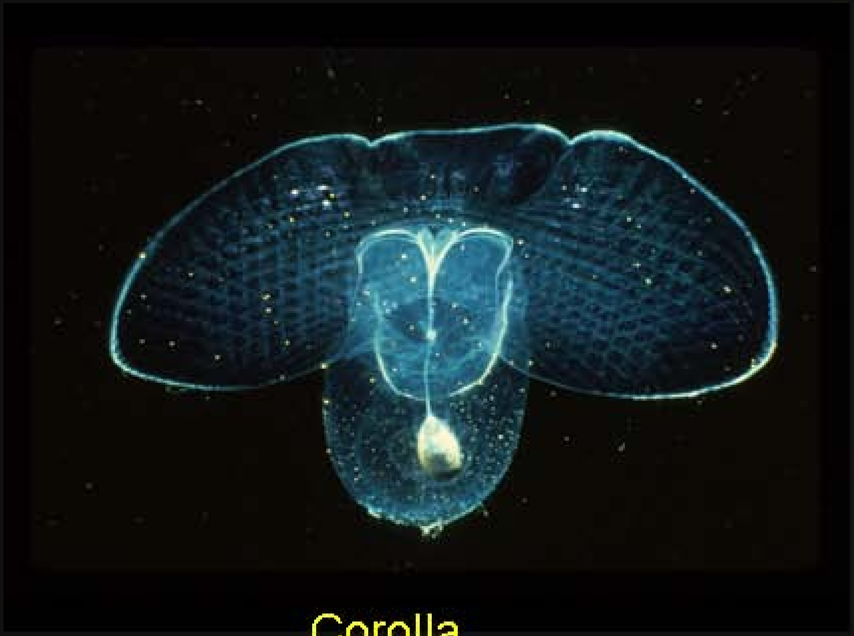
Group	Feeding Mechanism	Filtering rates	Particle retention
Appendicularians	External filtering house concentrates food, water flow by tail beat, mucous pharyngeal filter to collect ingest particles	~30 – 1000 ml h^{-1} $zooid^{-1}$	0.6 – 100 µm colloids too?
Doliolids	Mucous sheet on branchial basket, ciliary water pumping	0.3 – 21 ml h^{-1} $zooid^{-1}$	Non-selective, particles ≥ 0.2 µm
Salps	Unsupported internal mucous net, muscular water pumping	75 – 1429 ml h^{-1} $zooid^{-1}$	Non-selective, particles ≥ 2.0 µm
Pyrosomes	Mucous sheet on branchial basket, ciliary water pumping	4.6 ml h^{-1} $zooid^{-1}$; 5.5 - 35 l h^{-1} $colony^{-1}$	Non-selective, particles ≥ 10.0

Other gelatinous grazers

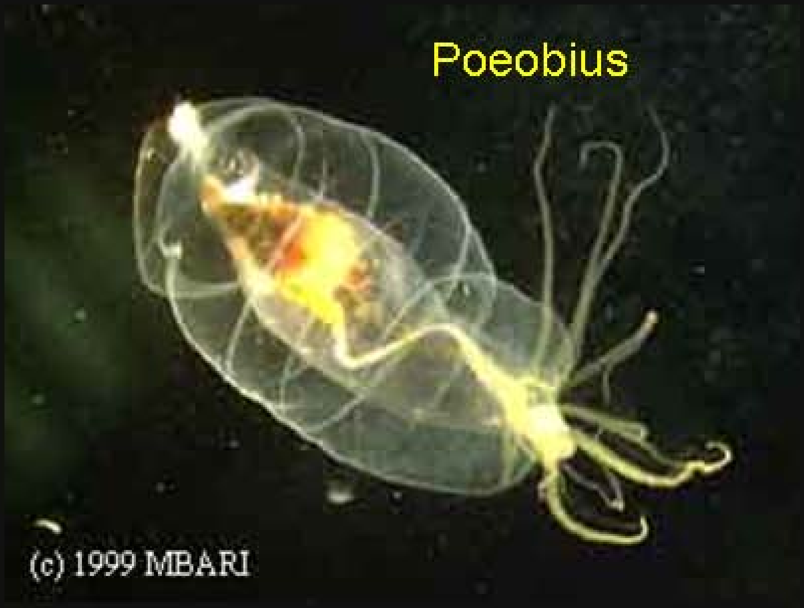
Pteropods

Pelagic holothurians

Particle feeding polychaetes



Corolla

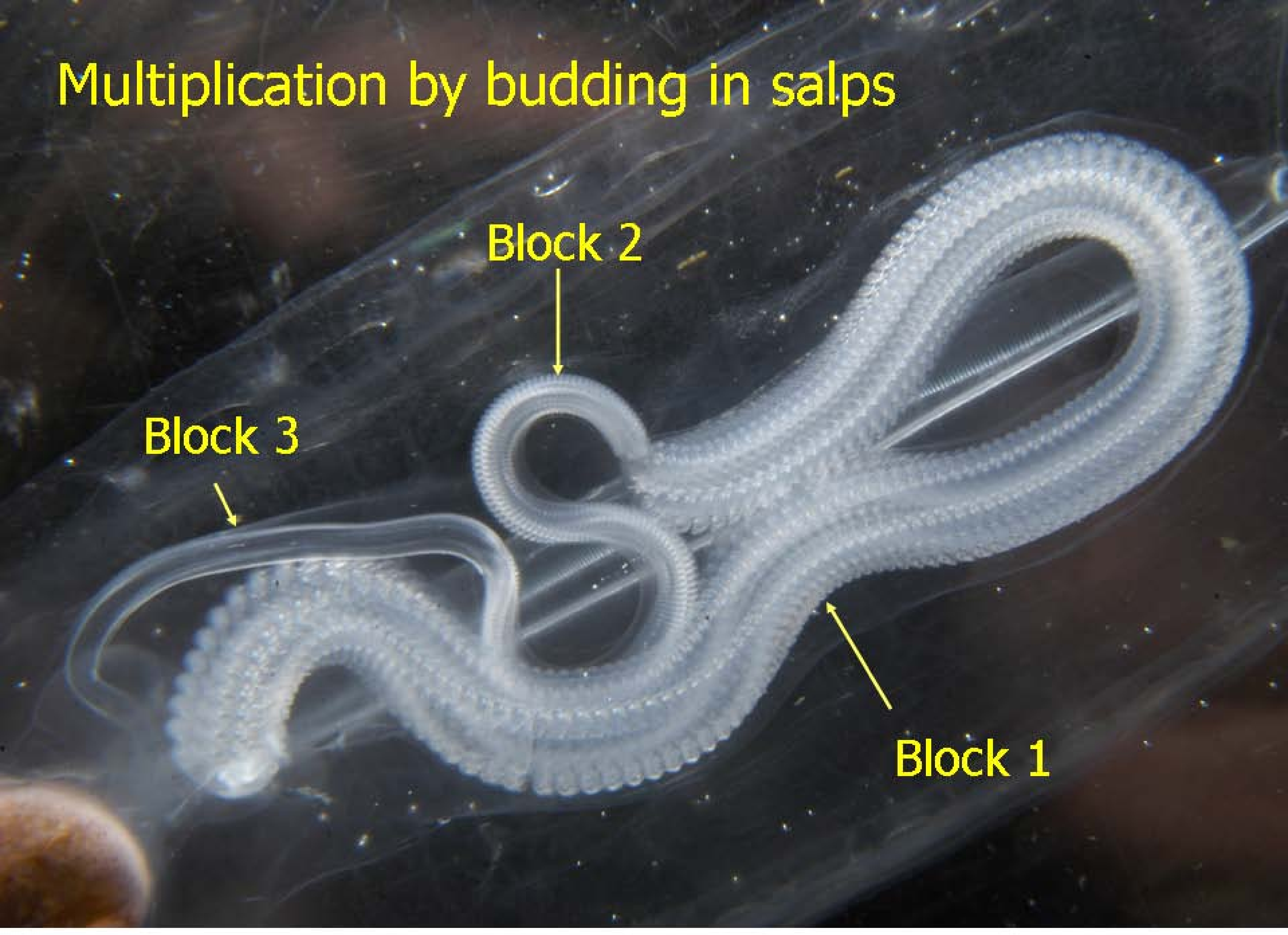


Why are the gelatinous grazers underestimated?

We need to know ‘how many and how fast’, but gelatinous grazers are:

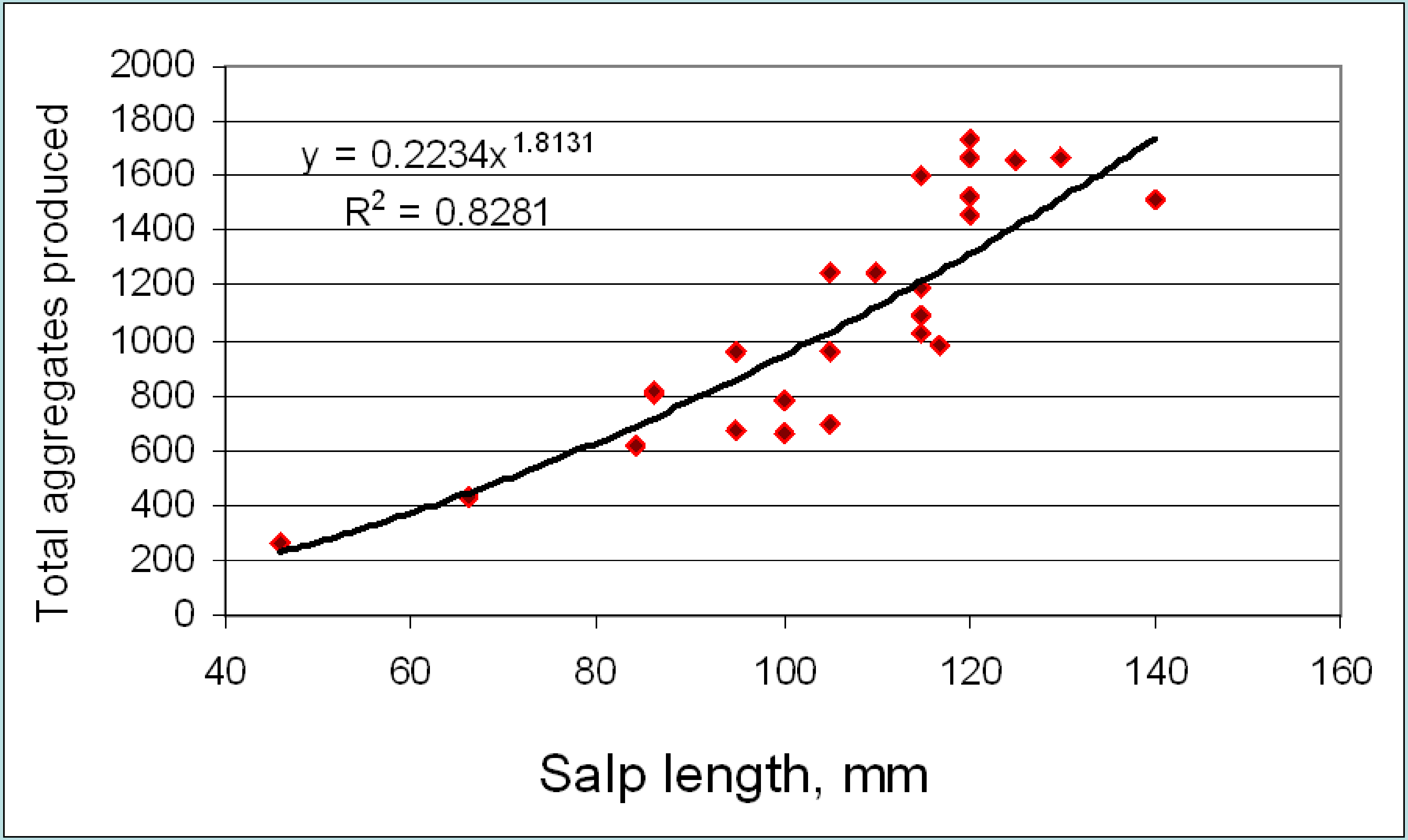
- fragile and hard to sample
- difficult to quantify
- frustrating to maintain for experimental work
- patchy with unpredictable distributions
- ‘nuisance’ factors in dense populations
- unfamiliar to taxonomists, with limited characters
- under-represented in zooplankton training

Multiplication by budding in salps



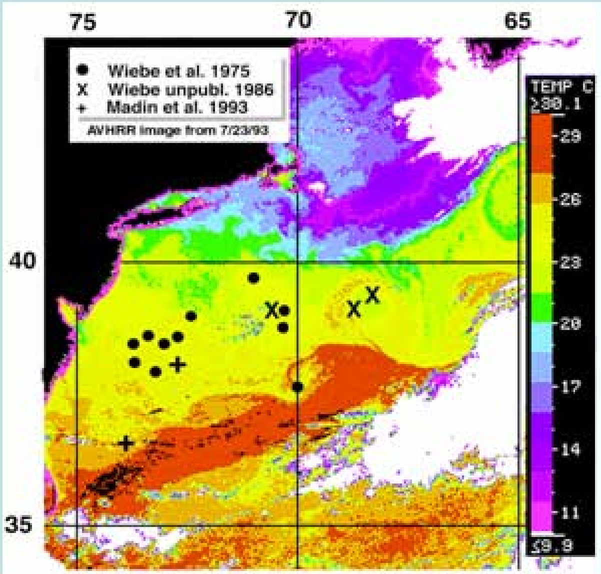
Asexual reproduction by *Salpa thompsoni*

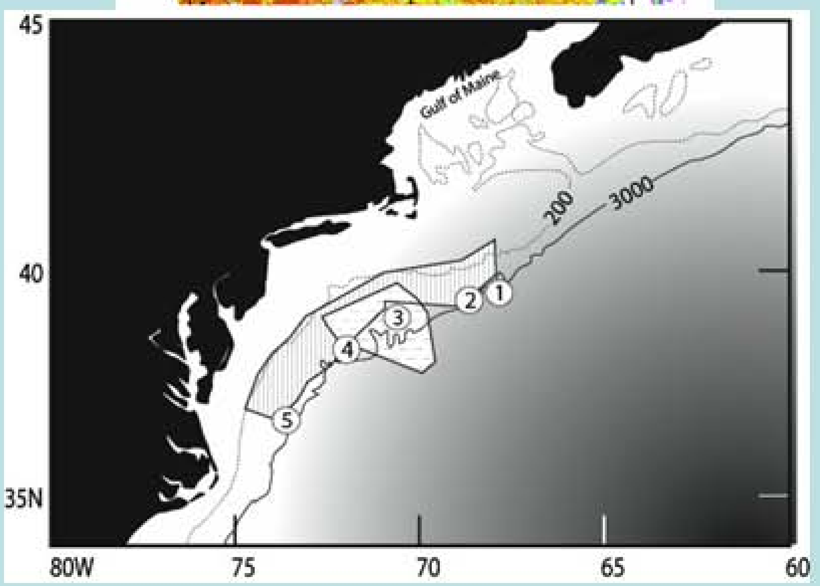
Aggregate offspring produced per solitary parent

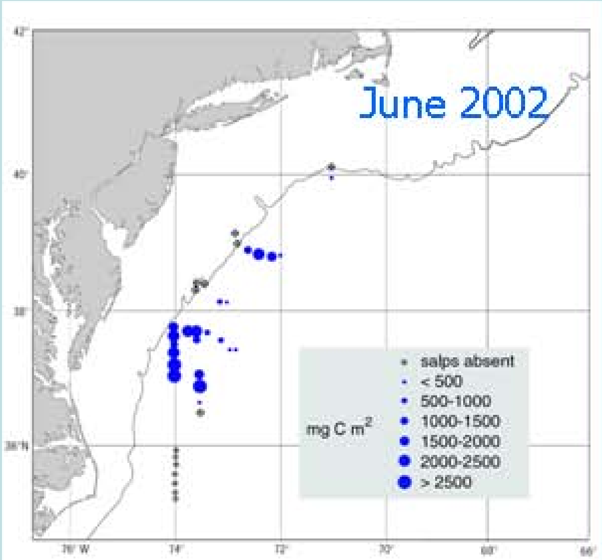


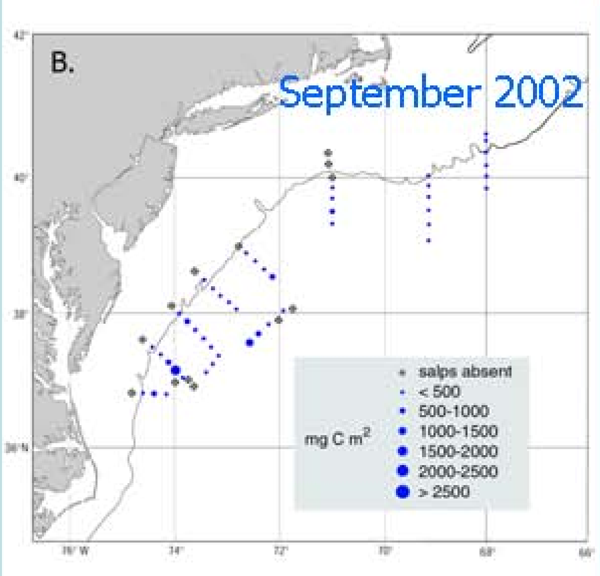
Madin et al, unpublished

Mid-Atlantic Bight: *Salpa aspera*



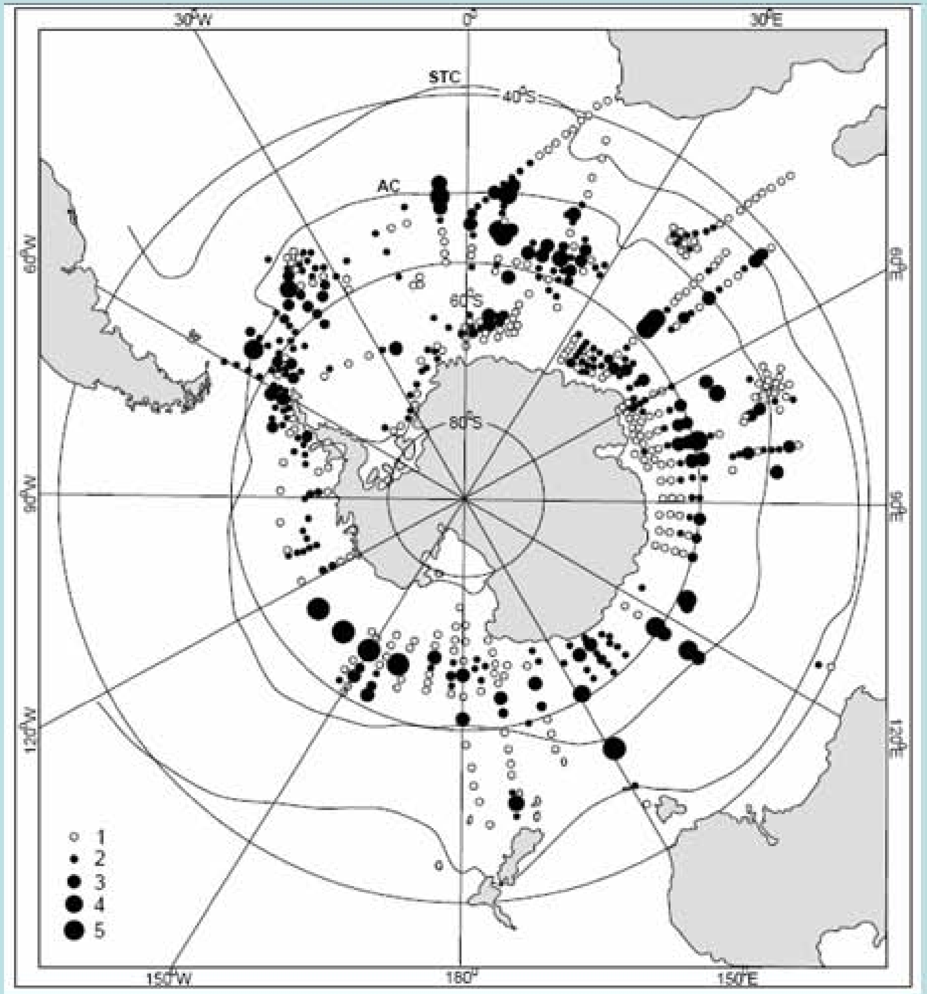






Salpa aspera surface swarm at night, Mid Atlantic Bight

Salpa thompsoni around Antarctica



Abundance key, salps per 20 minute tow:

1. Absent
2. 1-100
3. 101-1000
4. 1001-10,000
5. >10,000

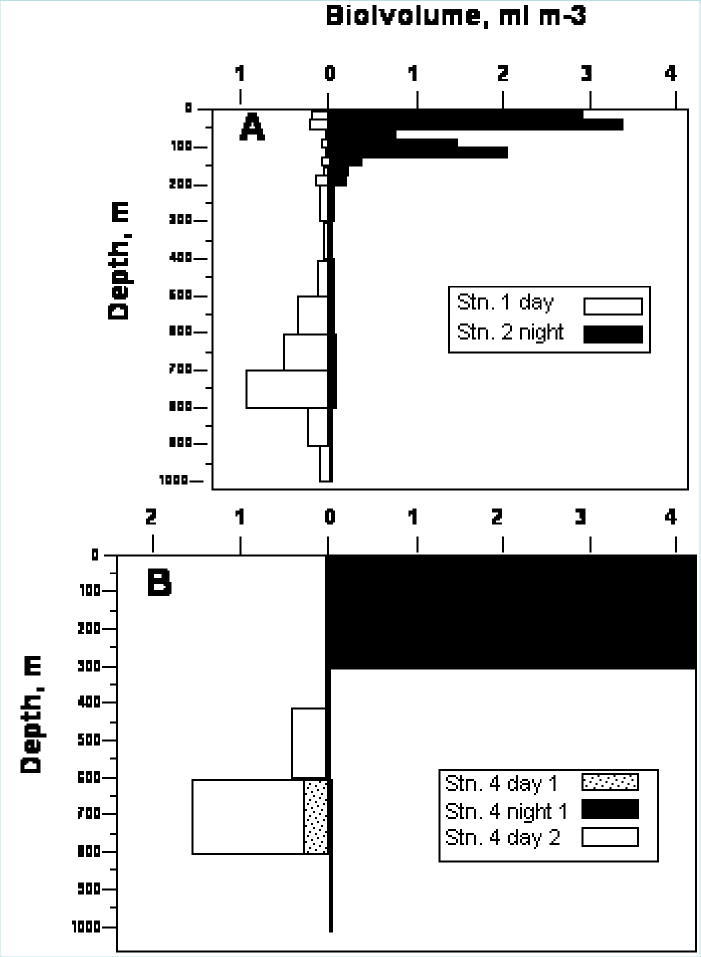
Pakhomov et al. (2002)

Species reported to swarm

Species	Locations	Maximum Density no. m-3
Dolioletta gegenbauri	Mediterranean, Georgia coast, California Current, Senegal Coast, Australia	4,000
Doliolum denticulatum	Mediterranean, Benguela Current, California Current	~10
Doliolum nationalis	Mediterranean, W. Atlantic, North Sea, Benguela Current	500
Cyclosalpa bakeri	Subarctic Pacific	30
Pegea confoederata	Bay of Bengal, Panama coast, Gulf of Aden, Arabian Sea	50
Salpa aspera	NW. Atlantic	65
Salpa cylindrica	Caribbean, Panama coast	~200
Salpa fusiformis	Mediterranean, NW Atlantic, NE Atlantic, Gulf of Guinea, California Current, New Zealand	1,000
Salpa thompsoni	Southern Ocean	~5
Thalia democratica	Mediterranean, NW Atlantic, Australia, New Zealand, California Current	1,000
Pyrosoma atlanticum	Mediterranean, NE Atlantic	40

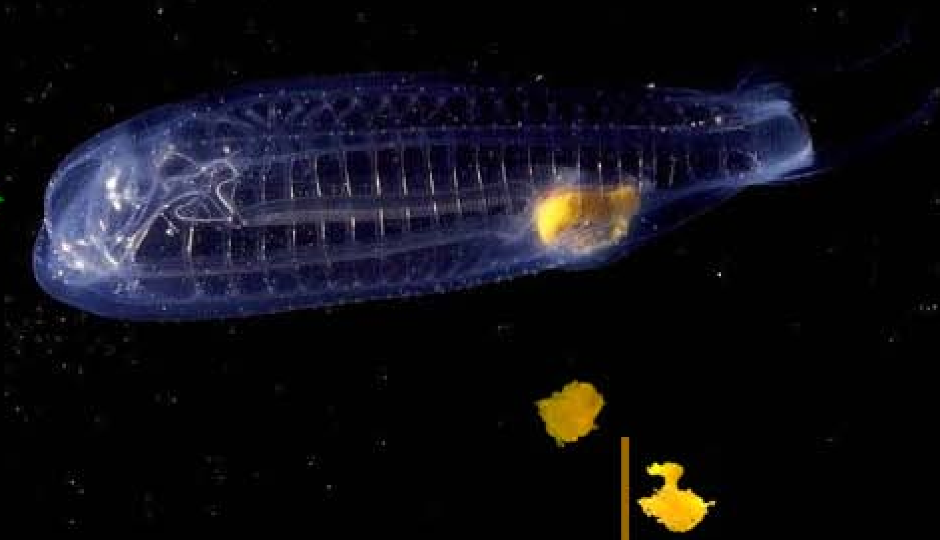
Diel vertical migration by salps

- ~10 species out of 45 are known to migrate
- Among the fastest and deepest migrating animals
- Migrations down to 800 m or more
- Night concentration in upper 50-100 m for feeding and reproduction
- Reverse migration sometimes occurs
- Salps hitting bottom can become prey for benthos
- Pyrosomes also migrate



Salps and vertical flux: the basic mechanism

Ingestion →



Primary production,
microzooplankton,
suspended detritus, etc.

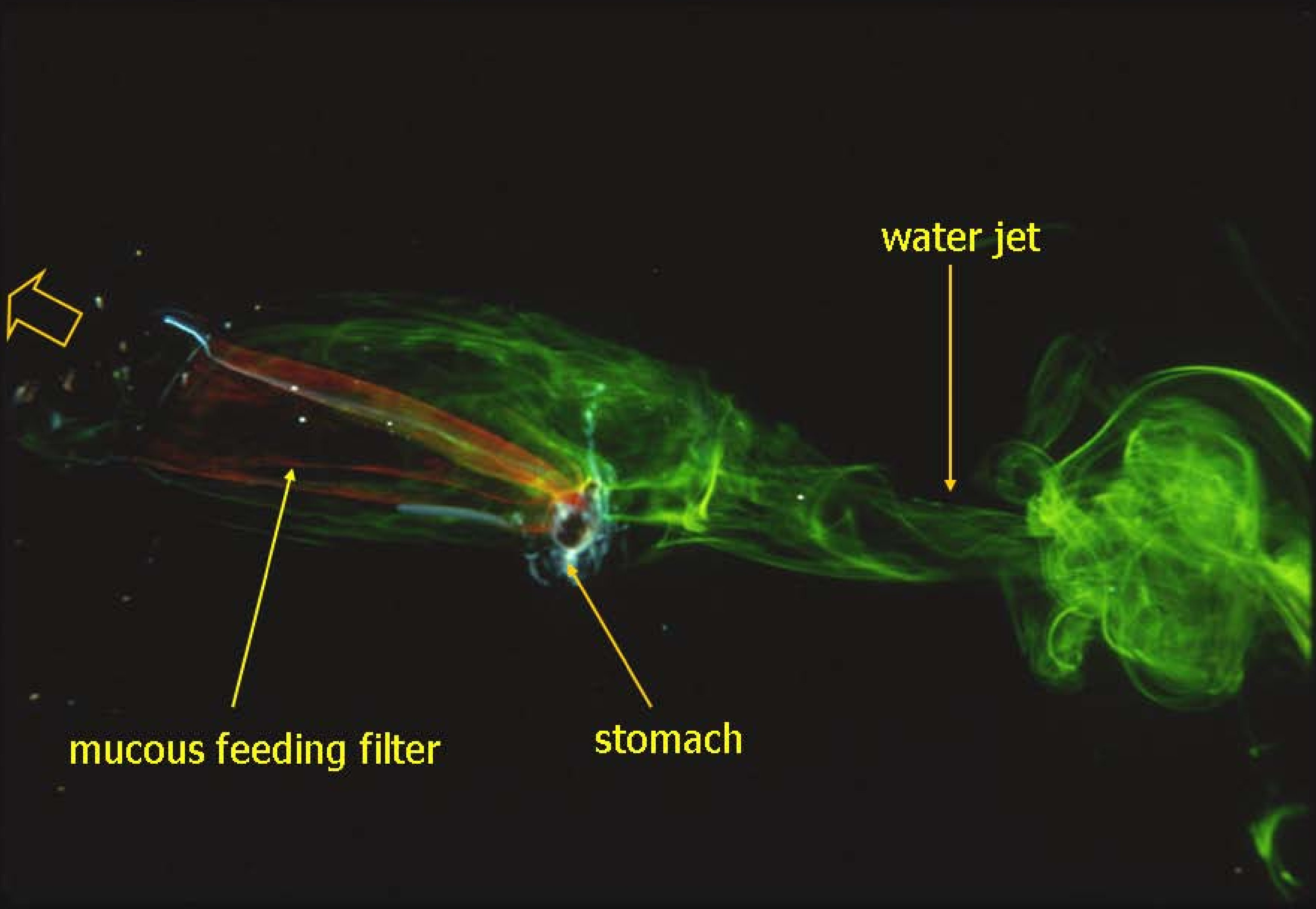
- Filter up to liters/hr
- Consume particles from 2 μm to 2 mm
- Produce large, mucus-wrapped fecal pellets
- Grow and reproduce rapidly
- Can form extensive, dense populations
- Some species migrate to 600+ m daily

Defecation ↓

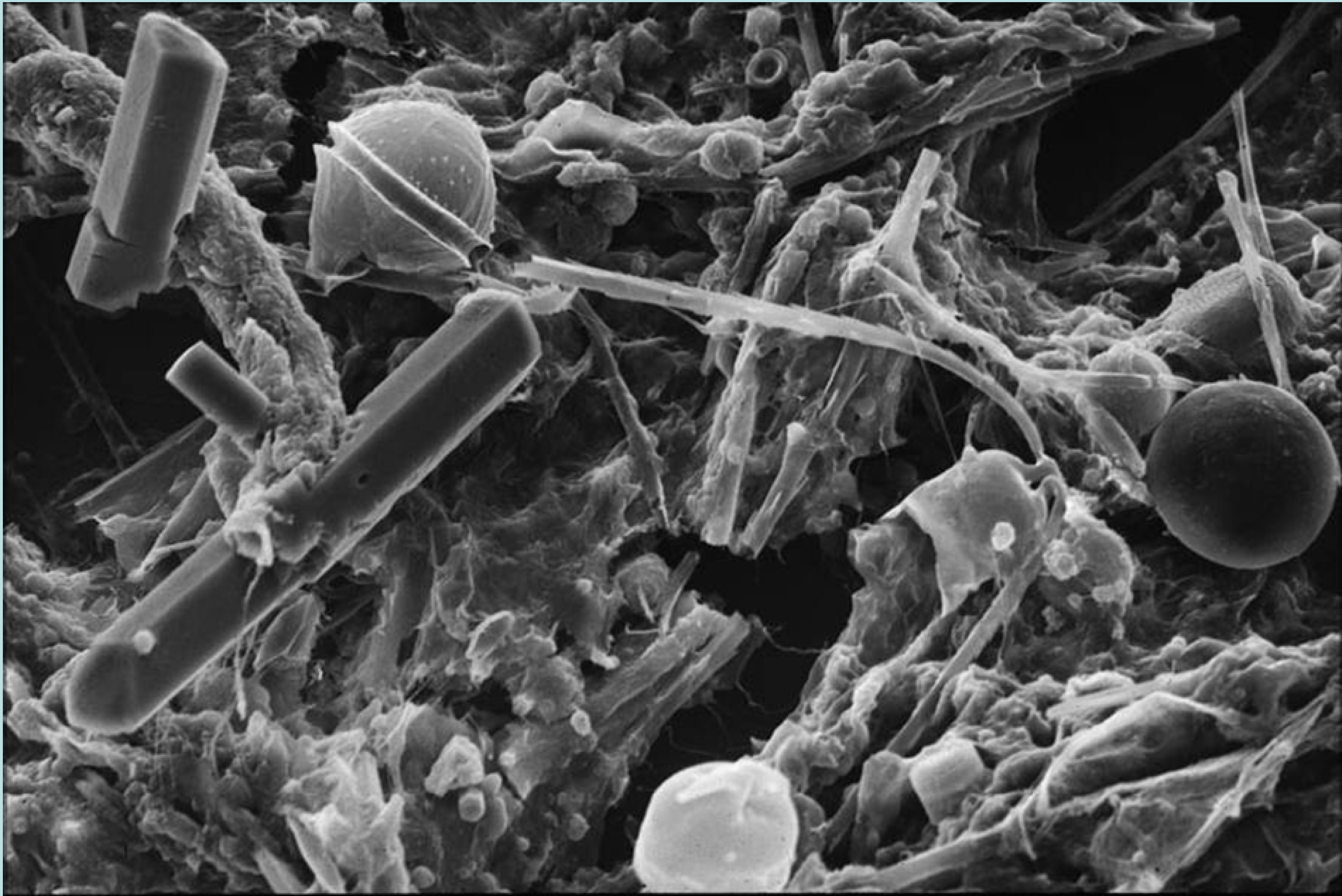
Carbon, nitrogen, Chl-*a*,
other pigments, etc.

Phytoplankton images: Lena von Harbou

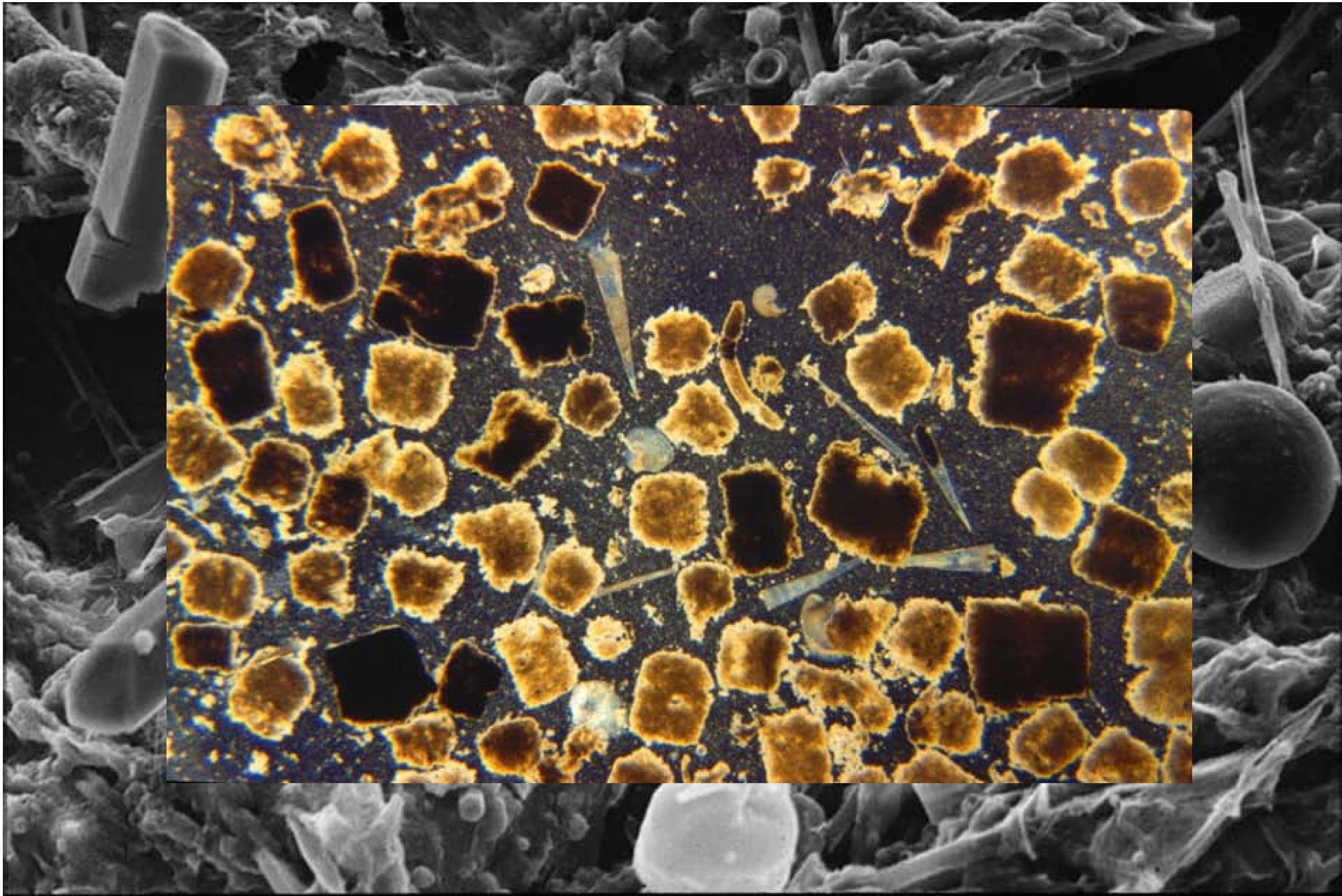
Slide design: Brennan Phillips


water jet
mucous feeding filter
stomach

From food to feces



From food to feces



Pellet Properties

Appendicularians
- Compact, cylindrical
- 300-500 µm long

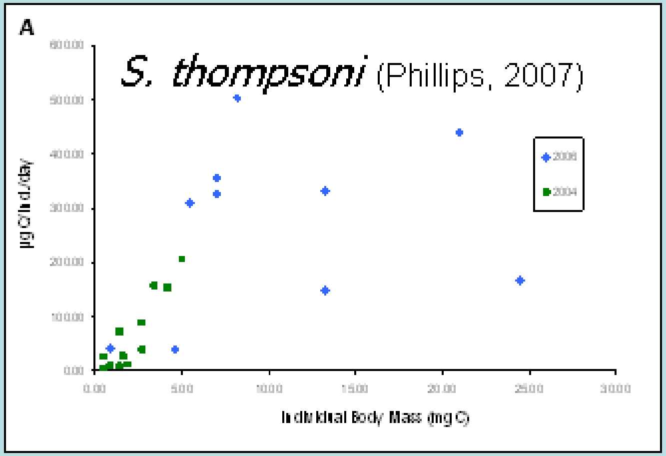
Doliolids
- Spheroidal to irregular
- 100 - 800 µm long
- C = 20% dw

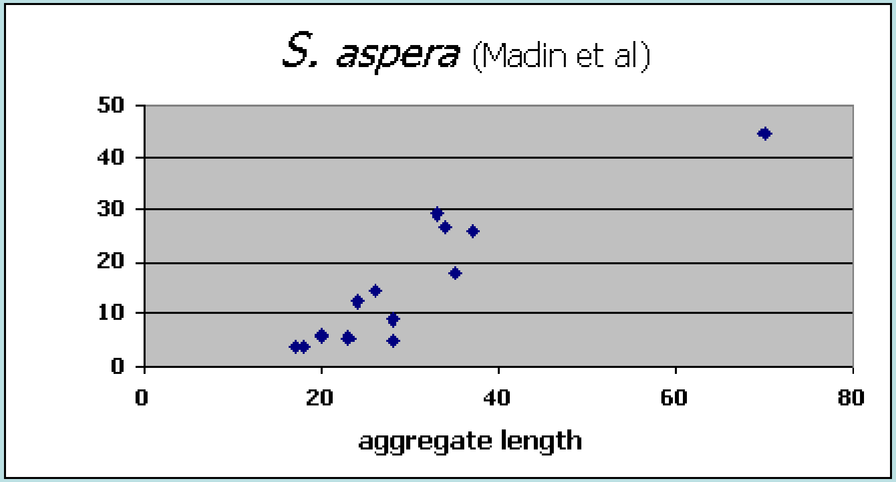
Pyrosomes
- Fusiform
- 250 µm long
- C = 22% dw

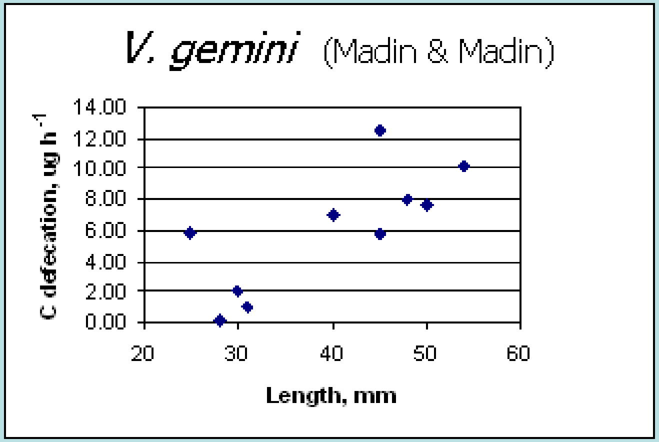
Salps
- Flattened, rectangular
- 1 - 5 mm long
- C = 25% dw

No microscope needed….

Estimates of fecal production rate
based on lab incubations







Fecal production for 3 species, as µg C salp^{-1} h^{-1}

Salpa thompsoni: 0.3 to 21 µg C

Salpa aspera: 1 to 45 µg C

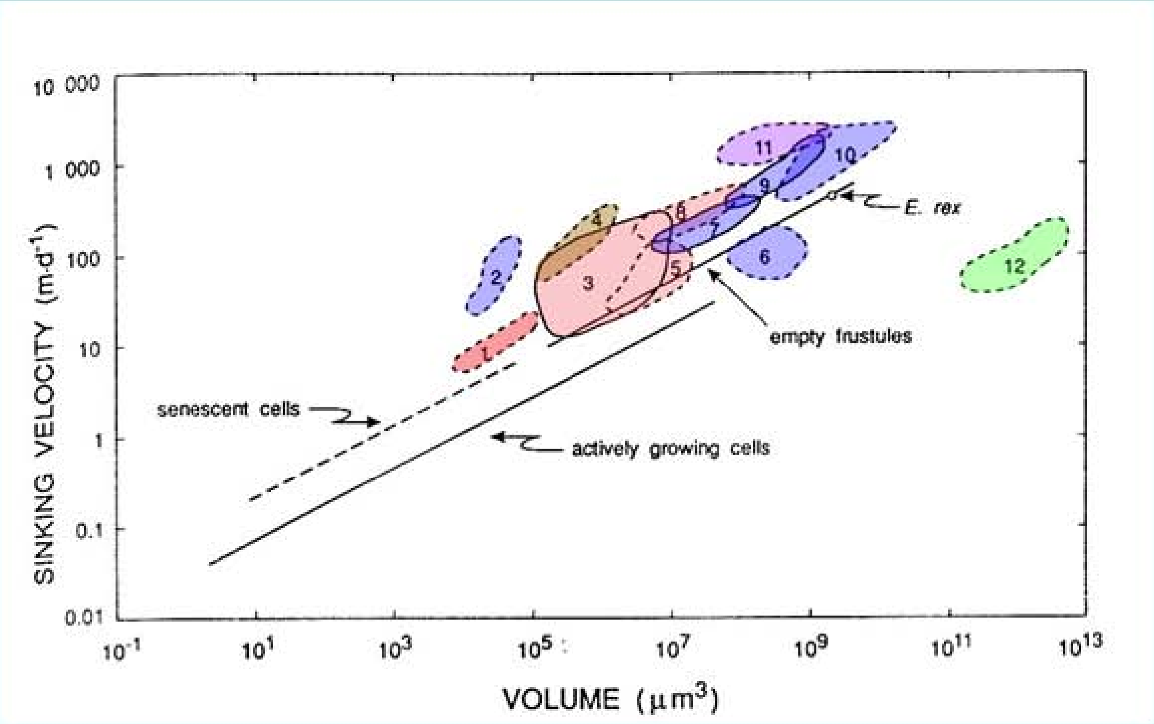
Vitreosalpa gemini: 0.1 to 12 µg C

Specific defecation rates, % body C d^{-1}

Mean of 7 species: 11.8 (Madin 1982)

S. thompsoni: 0.5 – 5.7 (Phillips et al 2007)

Pellet sinking velocities



1. nauplii & copepodites
3. copepods
5. *Pontella* sp.
8. Euphausiids

2. appendicularians
6, 7. Doliolids
9. *Corolla* (pteropod)
10. salps

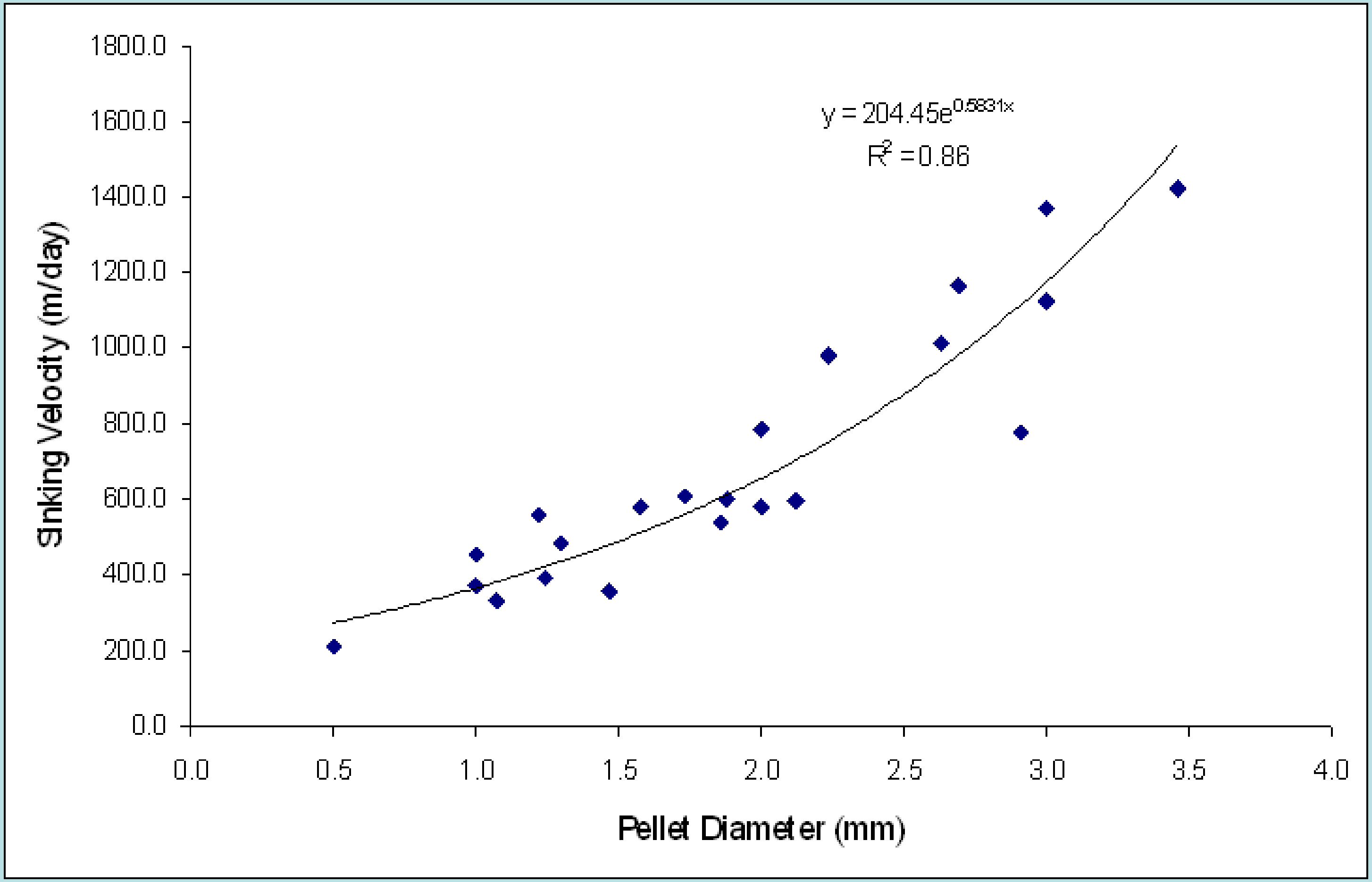
4. Unidentified natural

11. *Limacina* bodies

12. Diatom aggregates

Modified from Fortier et al. 1994, velocity data from various sources

Sinking rates for *S. thompsoni* pellets



(Phillips et al 2007)

Tunicate Pellet Sinking

Species	Pellet length mm	Sinking velocity m d^{-1}	Reference
Pyrosoma atlanticum	0.26	**51 - 89**	Drits et al. 1992
Salpa fusiformis	0.6	**48 - 139**	Yoon et al. 2001
Dolioletta gegenbauri	0.16 – 2.17	**59 - 405**	Deibel 1990
Oikopleura dioica	0.3	**25 - 518**	Gorsky et al 1984 Urban 1992
Cyclosalpa affinis	2.27	**119 - 593**	Yoon et al. 2001
unidentified	2 – 5	**400 - 900**	Ramaswamy et al. 2005
Cyclosalpa pinnata	3 - 13	**320- 950**	Madin 1982
Iasis zonaria	1.58	**790 - 1168**	Yoon et al. 2001
Salpa thompsoni	0.5 - 3.5	**200 - 1400**	Phillips et al 2007
Salpa maxima	3 - 7	**1210 – 1987**	Madin 1982
Pegea socia	3 - 4	**1797 - 2238**	Madin 1982

Salp Pellet Degradation

Pellet degradation experiment

- pellets from 5 species
- initial C content
- incubation 22° C for 1 d
- then 5° C for 9 d

Average results after 10 d:

- 22% C loss
- 31% N loss
- 20% sinking speed loss

Caron et al. 1989

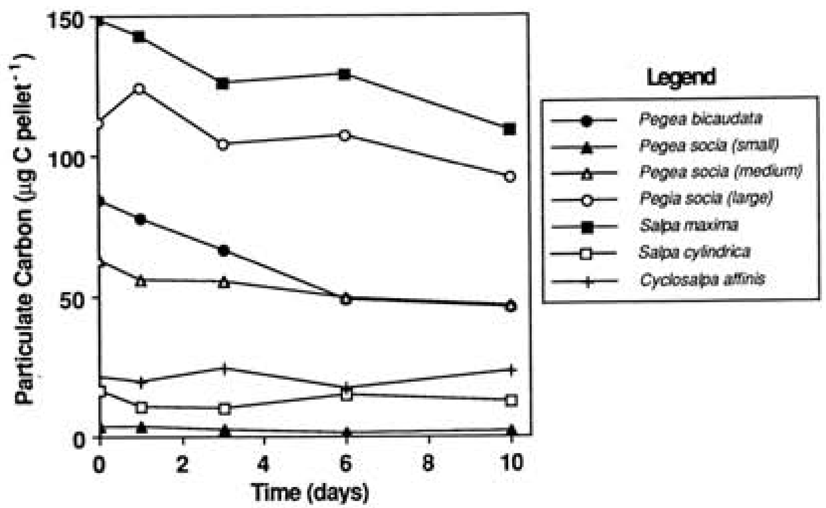


Figure 4. Time course of the loss of particulate carbon from seven groups of salp fecal pellets during a ten day decomposition experiment.

A slightly different story for *Pyrosoma* pellets:

- incubation 23° for 45 h: 59% C loss
- incubation 8° for 11 d: 0% C loss, significant loss of sinking speed and pigment

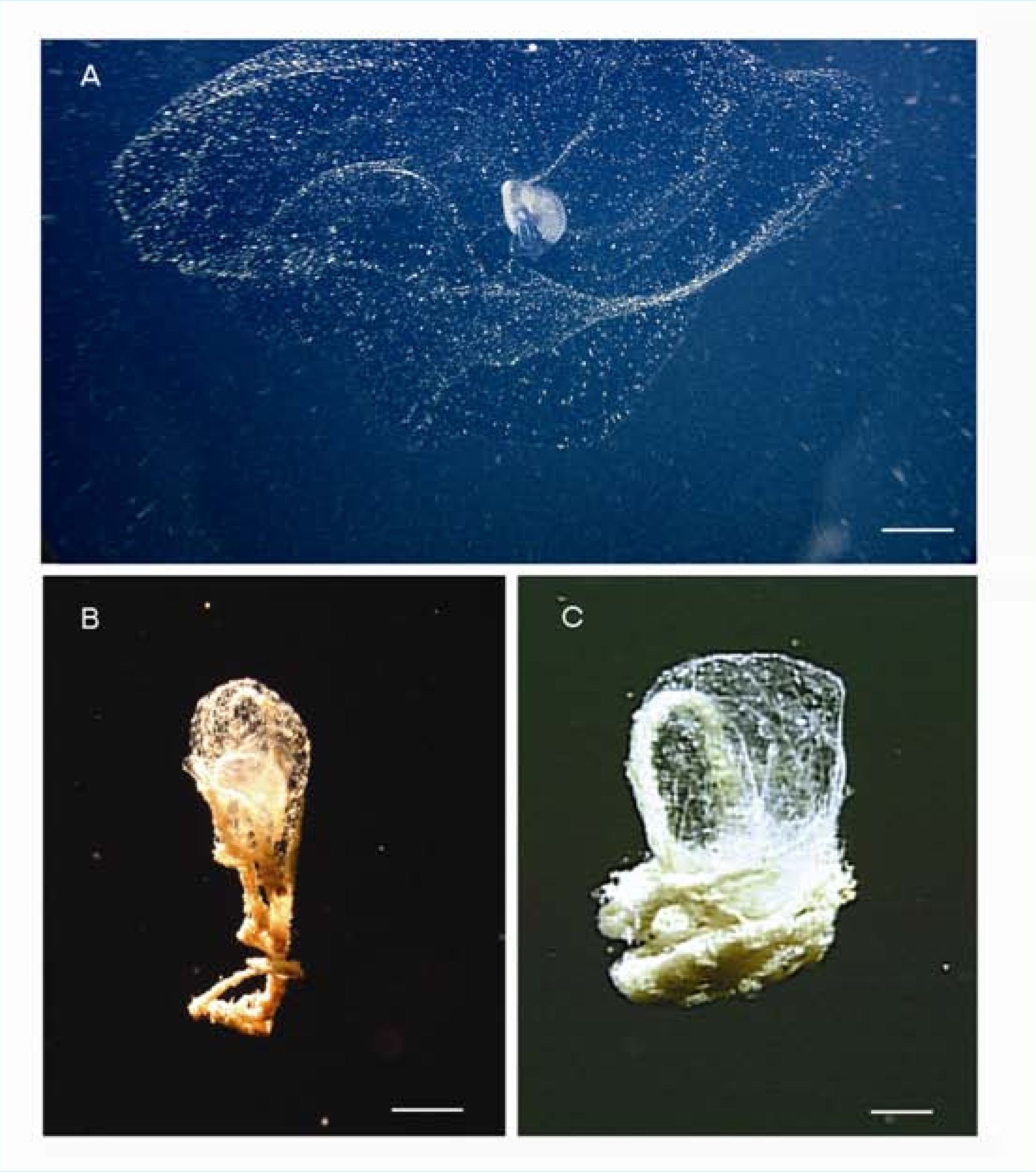
Drits et al. 1992

Examples of Fecal Flux

salps and pyrosomes

Species	Location	Method	Abundance no. m^{-2}	Biomass mg C m^{-2}	Fecal flux mg C m^{-2} d^{-1}	Reference
Salpa thompsoni	Southern Ocean	Direct measure	n.a.	863	42.3	Phillips et al. 2007
Salpa thompsoni	Lazarev Sea	Estimate from grazing	n.a.	n.a.	0.8 - 88	Perissinotto & Pakhomov 1997
Salpa aspera	Western N. Atlantic	Direct measure	n.a.	325 - 5713 ml m^{-2}	5 - 91	Madin et al. 2006
Salpa aspera	Western N. Atlantic	Estimate from biomass	6,500	909	8.5 - 137	Wiebe et al 1979
unidentified	Arabian Sea	Sediment trap, Th ratio	200 - 4,500	n.a.	332	Ramaswamy et al. 2005
Salpa fusiformis	Ligurian Sea	Sediment trap – 100 m	750	n.a.	576	Morris et al 1988
Salpa fusiformis, Thalia spp..	West of Baja California	Estimate from biomass	113 - 43,000	2 – 2050	1 - 609	Hereu et al 2006
Cyclosalpa bakeri	Subarctic Pacific	Direct measure	55 - 1,842	76 - 3621	21 - 875	Madin et al. 1997
Pyrosoma atlanticum	Eastern N. Atlantic	Direct measure	8 - 400	n.a.	87 - 1035	Drits et al. 1992

Flux by giant Appendicularian Houses



Bathochordaeus spp. Produce mucous houses up to 1 m diameter

House production estimated at 1 d^{-1}

Abandoned houses collapse and sink at up to 900 m d^{-1}

Estimated annual flux rate of 7.6 g C m^{-2} yr^{-1}

Sinker flux is 50-100% of sediment trap C flux at seafloor

Other new species of large mesopelagic appendicularians found in recent years.

(Robison et al 2005)

Roles of Gelatinous Grazers

Rapid and dominant grazing impacts
- High growth and reproduction
- Broad particle selection
- High filtration rates

→ all pelagic tunicates, some pteropods

Mixed layer recycling
- Fast production of small fecal pellets and small appendicularian houses

→ appendicularians, doliolids, small salps, pyrosomes

Vertical flux
- Large, fast sinking pellets resistant to degradation, accelerated by diel migration

→ appendicularians, salps, pyrosomes

Some other ecosystem effects

- Competition with other grazers
  - Copepods, krill
- Consumption of microzooplankton, larvae
  - Protists, nauplii, pteropods
- Substrate and food source
  - Microbes on houses, pellets
  - Amphipods & copepods as symbionts
  - Medusae, fish, turtles as predators
- Sinking carcasses
- Climate responses and impacts
  - Ice effects in Southern Ocean (Loeb et al 1997)
  - DMS production? (Kasamatsu et al 2004)

Will salps save the climate?

Transparent Animal May Play Overlooked Role in the Ocean

The daily journal of life in and around water
UnderwaterTimes.com

Jellyfish-like 'Salps' May Play Major Role in Fate of Carbon dioxide in the Ocean

GEO-ENGINEERING USING SEA-CREATURES: ANOTHER POTENTIAL FIX FOR ANY GLOBAL WARMING

FOX NEWS.com

Jellyfish-Like Sea Creatures Fight Global Warming

BBC NEWS

Sea creatures' global warming fix

Sea Creature Does Its Part to Purge Pollution

The Royal Gazette

Entrepreneur defends greenhouse gas removal plan

May 1, 2007
The Energy Challenge
Recruiting Plankton to Fight Global Warming

Jellyfish Squish Greenhouse Dogma

Summary points

- Pelagic tunicates are efficient, high-throughput grazers on a wide range of particles
- Salps in particular form large, dense fecal pellets that sink at 200-2500 m d^{-1}
- Tunicates can grow rapidly and form dense populations under favorable conditions
- Diel migration to 800+ meters accelerates downward flux
- Midwater salps, doliolids and appendicularians repackage detritus and accelerate its sinking
- These processes constitute a natural and ongoing sequestration of fixed carbon in the ocean
- Future responses to elevated CO_2 and/or primary production in the ocean remain to be observed – but activity of grazers will be essential for any enhanced sequestration schemes