

Feeding Relationships

- Modeling feeding:
Functional response relationships
- Factors resulting in selective feeding



Measures of Feeding Rates

Clearance Rate (F)

volume cleared * predator⁻¹ * time⁻¹
(e.g., *nl flagellate⁻¹ h⁻¹*)

Specific Clearance Rate

volume cleared * predator biovolume or biomass⁻¹ * time⁻¹
(e.g., by volume: *h⁻¹*; by biomass: *nl pg C⁻¹ h⁻¹*)

Instantaneous Prey Mortality (or specific mortality rate)
("m" but also known as "g")
time⁻¹ (*d⁻¹*)

Derived from:

$$P_t = P_0 * e^{-mt}$$

where: $m = F * D$

and $D = \text{predatory density (\#/vol)}$

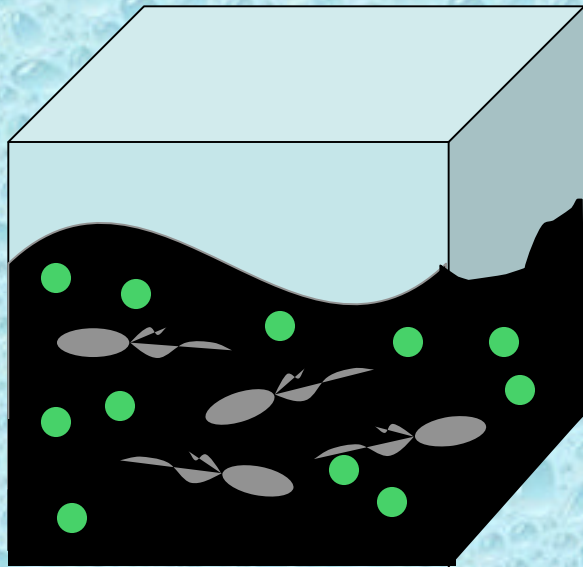
Ingestion Rate (I)

number or biomass of prey consumed * predator⁻¹ * time⁻¹
(e.g., *bacteria flagellate⁻¹ h⁻¹*)

$$I = F * C$$

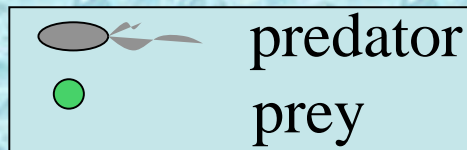
where $C = \text{mean prey density}$

Clearance Rate Concept



$$\text{Clearance Rate (F)} = \text{Volume cleared of prey pred}^{-1} \text{ time}^{-1}$$

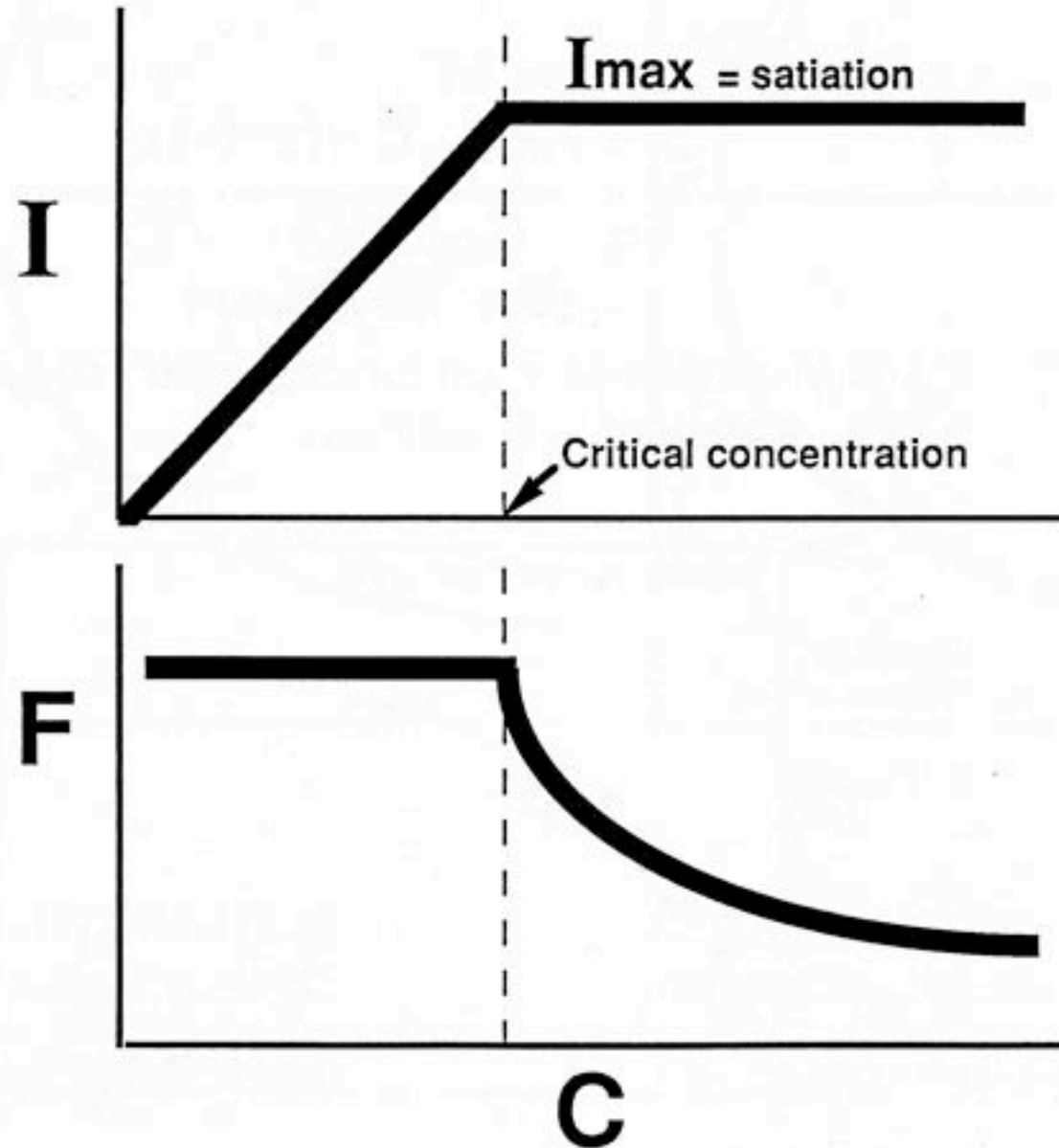
A consumer may have different F for different prey types being fed upon at the same time.



Relative F is a measure of capture efficiency or “selectivity”.

Ingestion (I) = F x C,
where C = avg. prey concentration

Functional Response - Type 1



Sustained F_{\max} to critical concentration, then reduced F to maintain I_{\max}

Feeding on diatoms by the copepod, *Calanus pacificus*

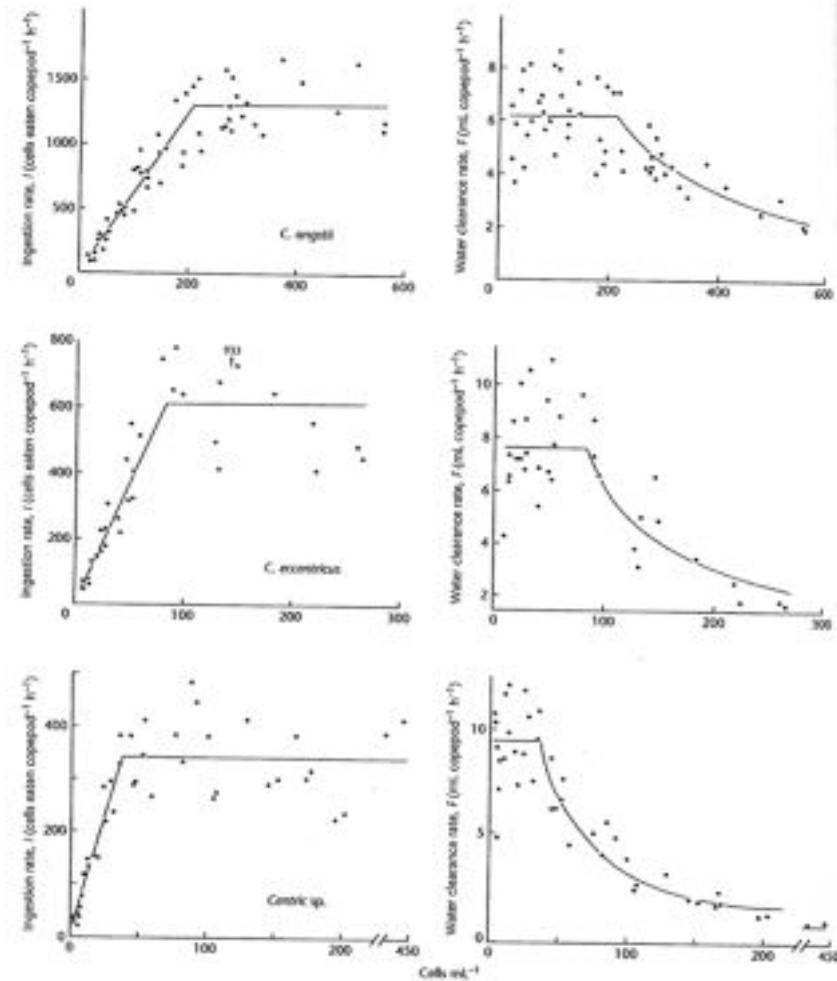


Fig. 7.4 Effect of cell concentration on ingestion rate (I , cells eaten copepod⁻¹ h⁻¹, left) and water clearance rate (F , ml copepod⁻¹ h⁻¹, right) in *Calanus pacificus* females feeding on three small-, medium-, and large-sized diatoms. (After Frost 1972.)

Non-linear Functional Response (Type 2)

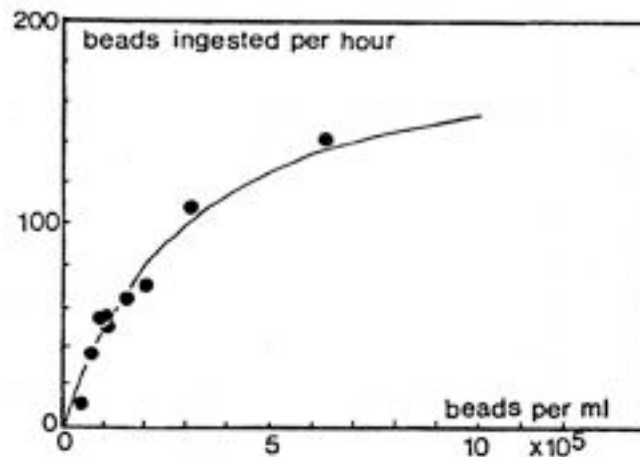
Model:

from $I = F \cdot C$
and $t' = \text{food handling time}$

then $I_{\max} = 1/t'$
 $I = F_{\max} \cdot C \cdot (1 - t' \cdot I)$

$$I = \frac{(I_{\max} \cdot C)}{(C + I_{\max}/F_{\max})}$$

I = Michaelis-Menton function with 1/2-saturation constant = I_{\max}/F_{\max}

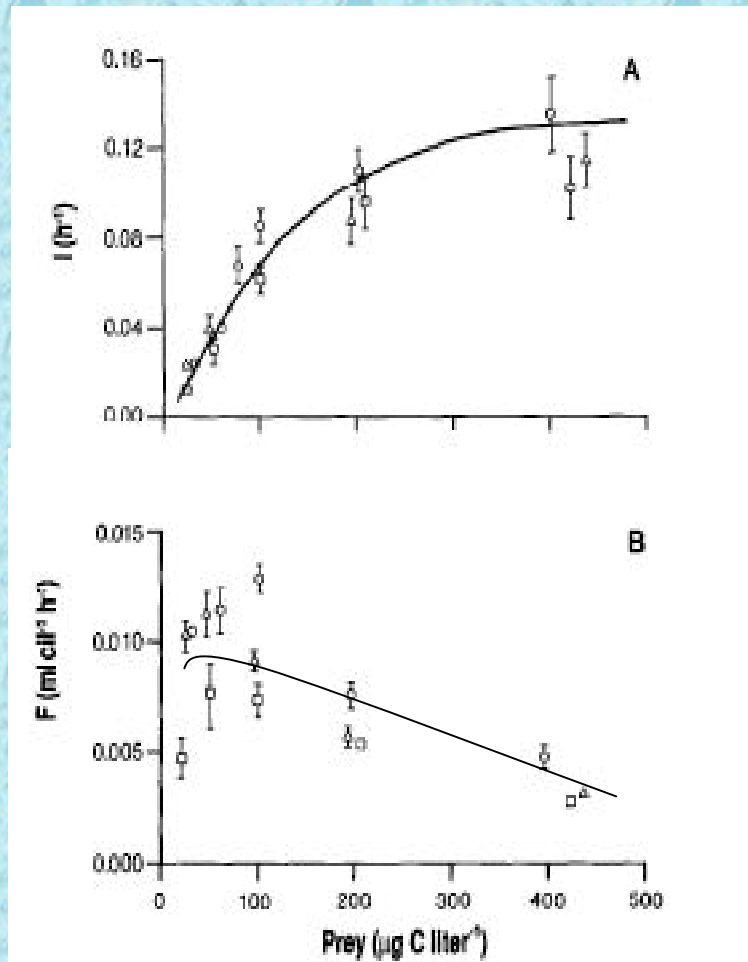


Uptake of 2- μ m latex beads by the oligotrich *Halteria grandinella* as a function of bead concentration. Data fit to hyperbolic function. Slope at origin = $F_{\max} = 0.7 \mu\text{l/h} = 8 \times 10^4 \text{ body volumes/h}$ (From Fenchel, 1986a).

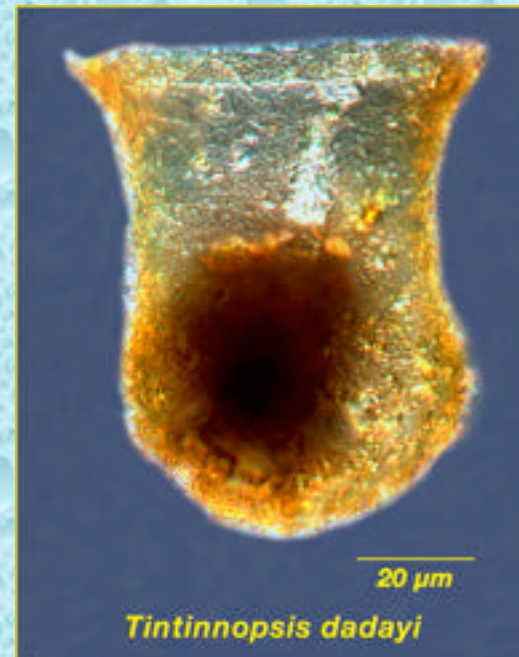
Assume: existence of a prey handling constraint: e.g., the rate limiting step for feeding in protists is the rate of recycling of vacuole membrane material.

For metazoans, it still takes time to process food and not all organisms in a population behave exactly the same way: both of these factors lead to a curvilinear relation.

Ciliate: functional response curves



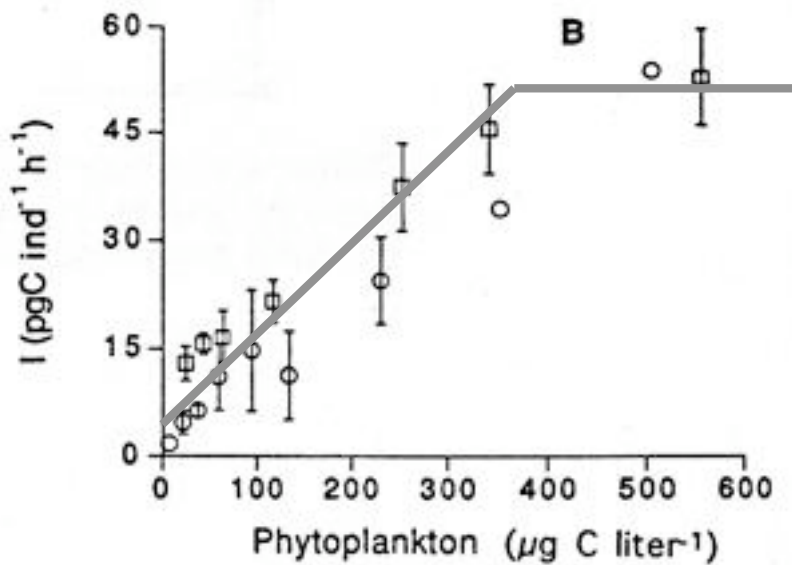
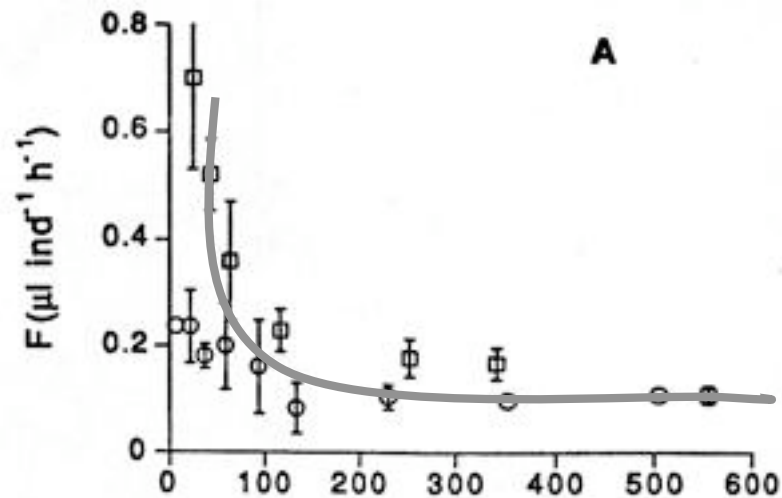
Tintinnopsis fed phytoplankton



www.obs-vlfr.fr

Verity 1991

Pallium feeding: same functional response curves



Dinoflagellate feeding on diatom

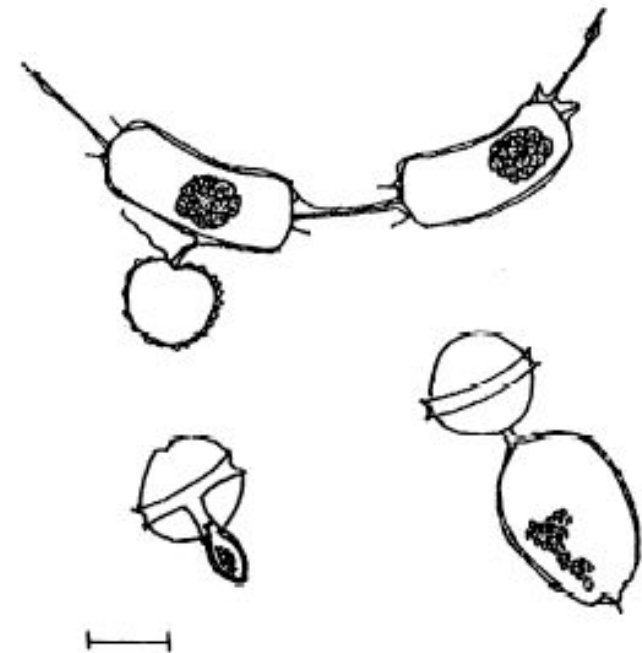
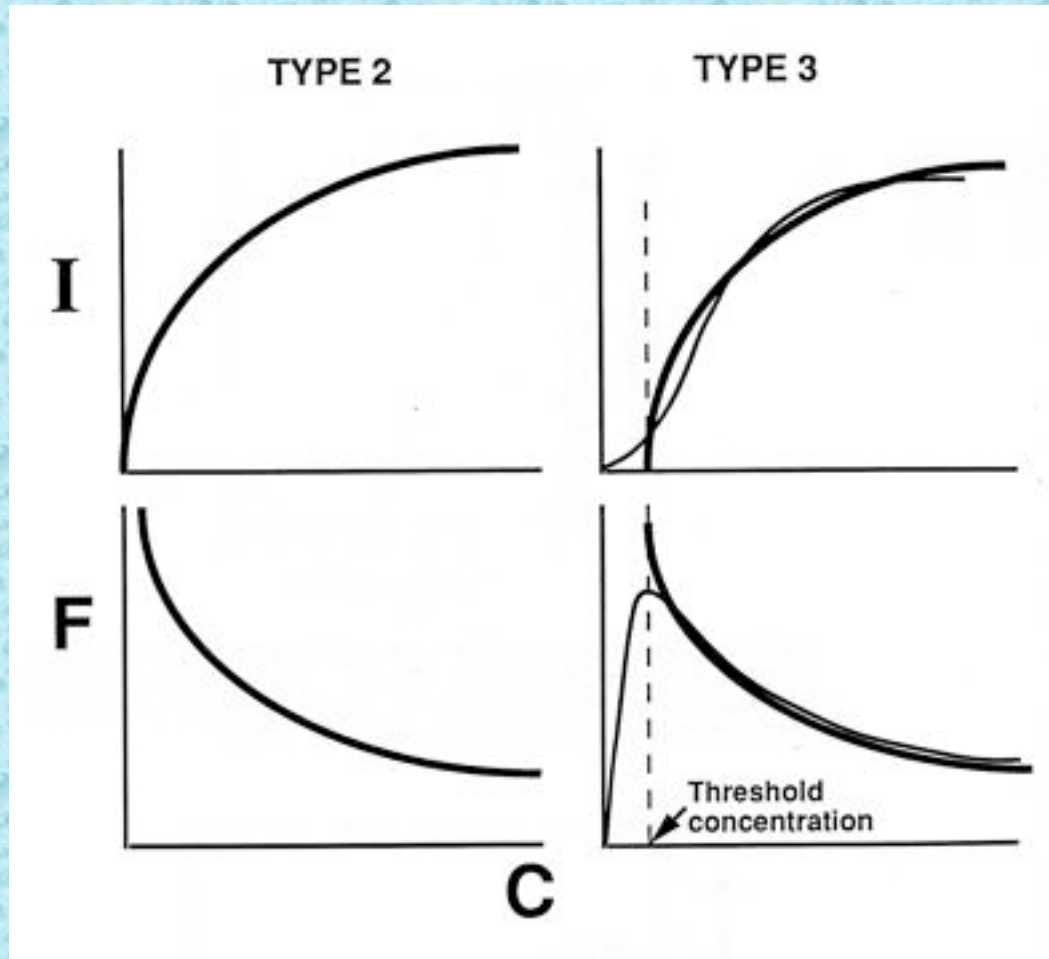


Fig. 1. *Obilea rotunda* with captured, pallium-ensheathed cells of (clockwise from top) *Ditylum brightwellii*, *Prorocentrum micans*, and *Pyrenomonas salina*. Scale bar—20 μm .

Strom & Buskey 1993

Functional Response: Types 2 & 3



UNSTABILIZING

Highest F at low C

*Prey handling time reduces
clearance efficiency*

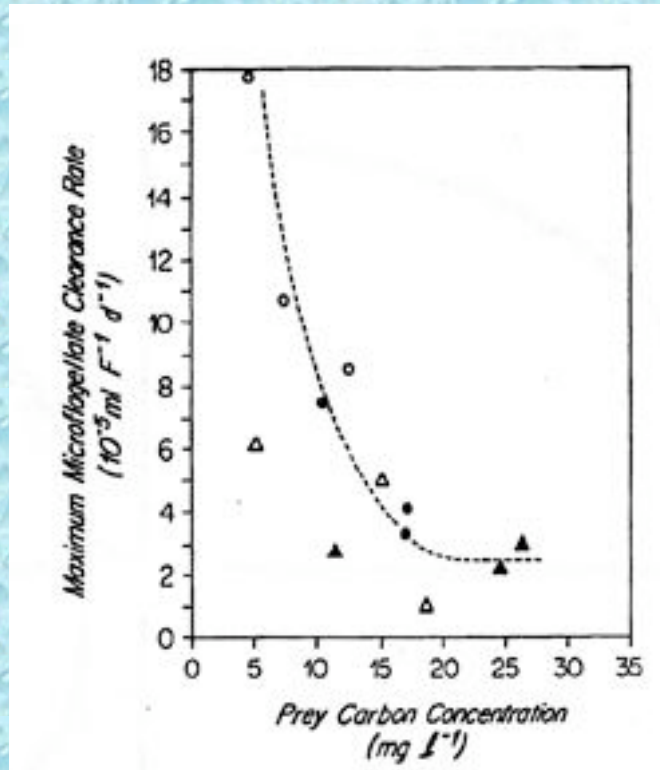
STABILIZING

Reduced feeding at low C

*Energetic efficiency
Prey refuge from predation*

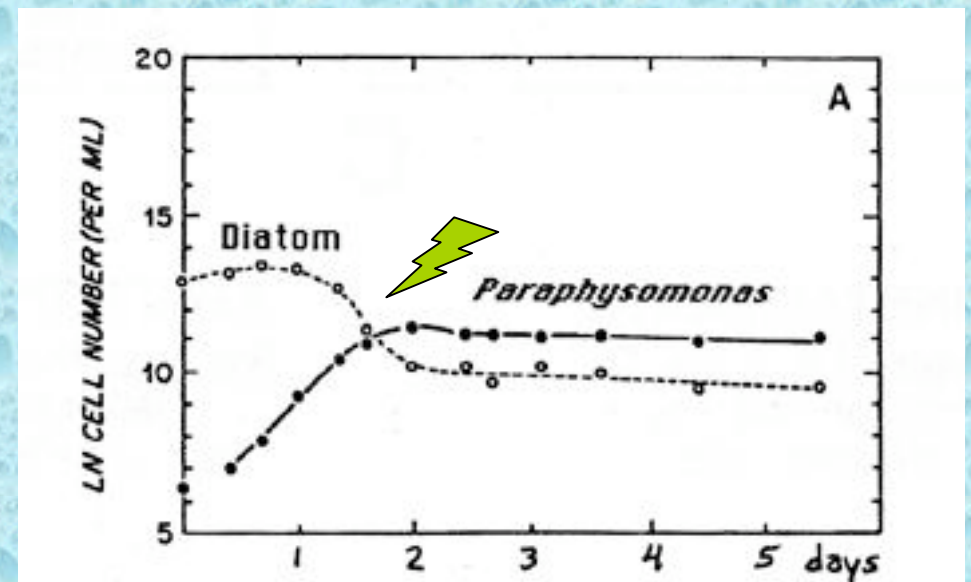
Threshold Feeding?

flagellate feeding on diatom and chlorophyte



Goldman et al. 1987

flagellate feeding on diatom

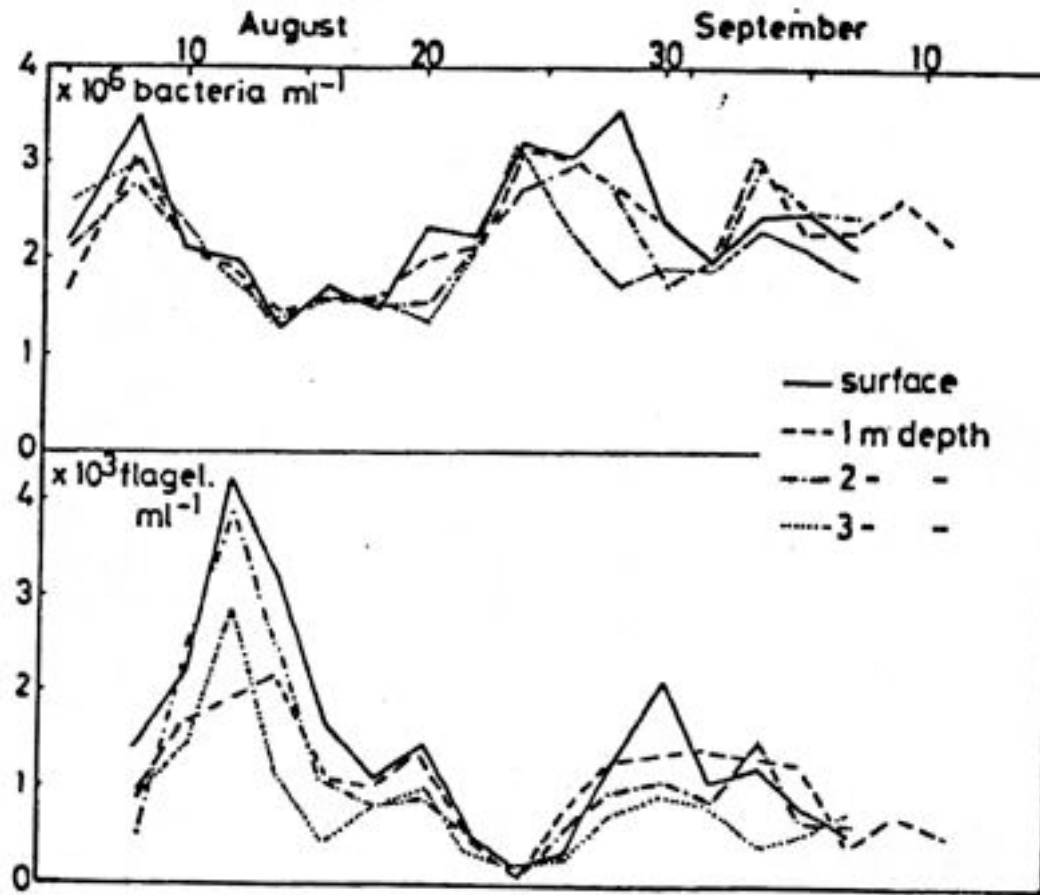


Goldman & Caron 1985

Grazing Thresholds and Predator-Prey Cycles

bacteria
abundance

flagellate
abundance



Fenchel 1982

Non-feeding Protists?

- Starvation-survival mode
 - Encystment
 - Decrease metabolic rate (next week)
- OR
- Switch to different prey type?
- Switch from phagotrophy to autotrophy?

Non-feeding Copepods? Starvation Response

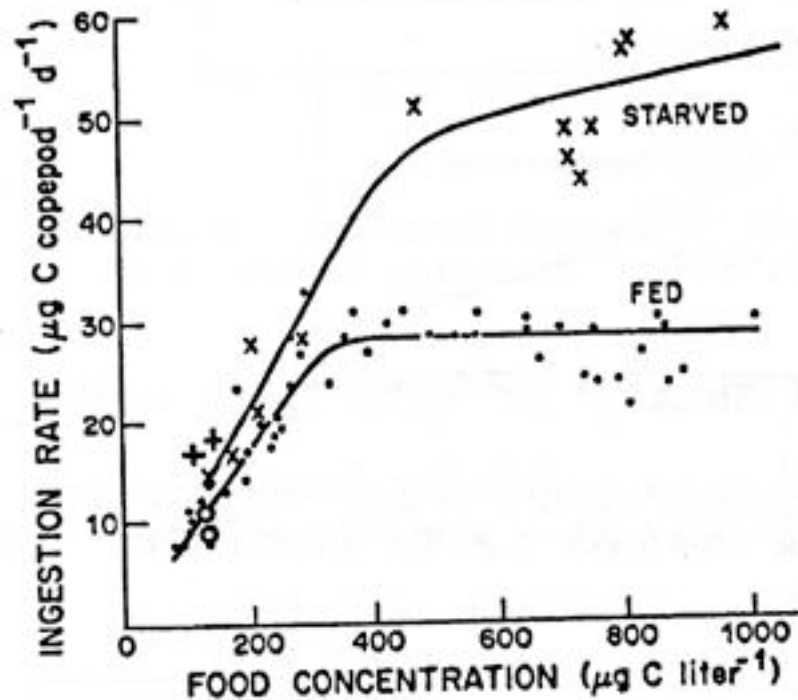
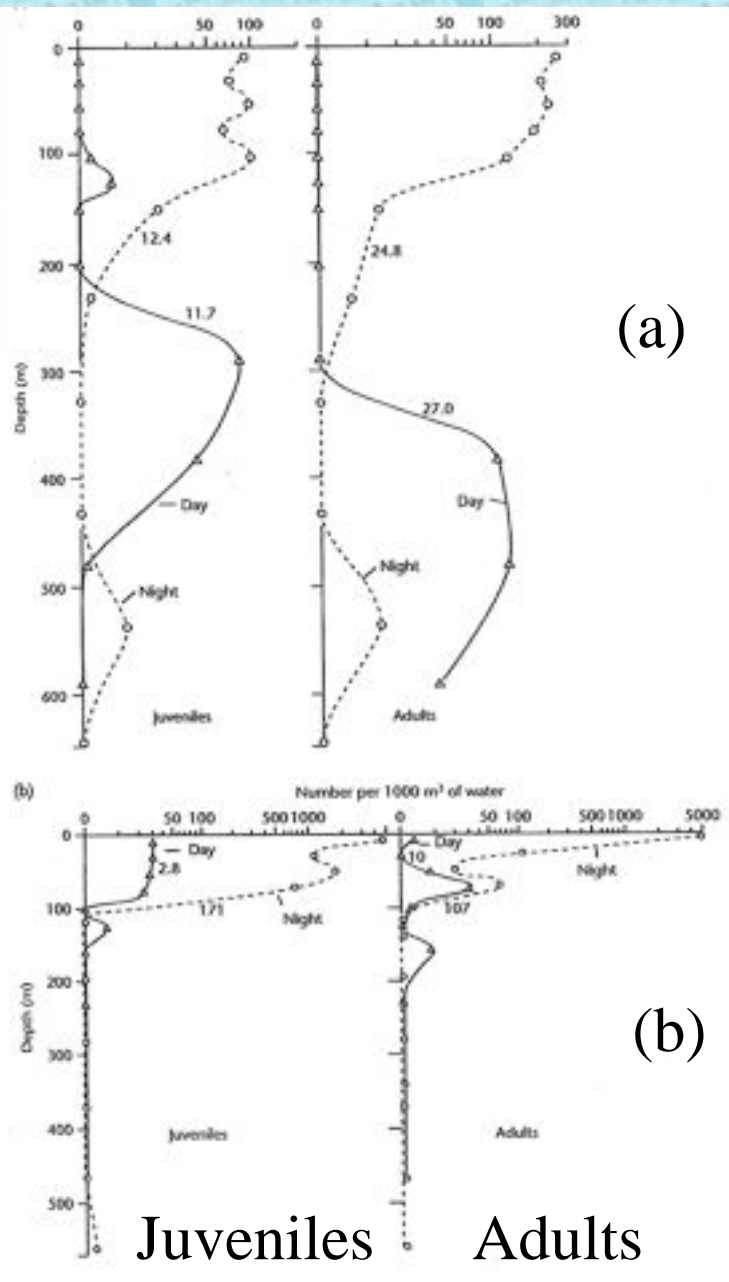


Fig. 4. Starvation-enhanced feeding of *Calanus pacificus* females on the diatom *Thalassiosira weissflogii*. Ingestion rates of previously fed and starved copepods represented, respectively, by "•" and "X" from Frost (1972) and "O" and "+" from Runge (1980). Curves were fitted by eye.

From: Landry & Hassett. 1985. Time scales in behavioral, biochemical, and energetic adaptations to food-limiting conditions by a marine copepod.

Other non-feeding behaviors

- In some organisms, get Diel Vertical Migration behavior -- feed only at night



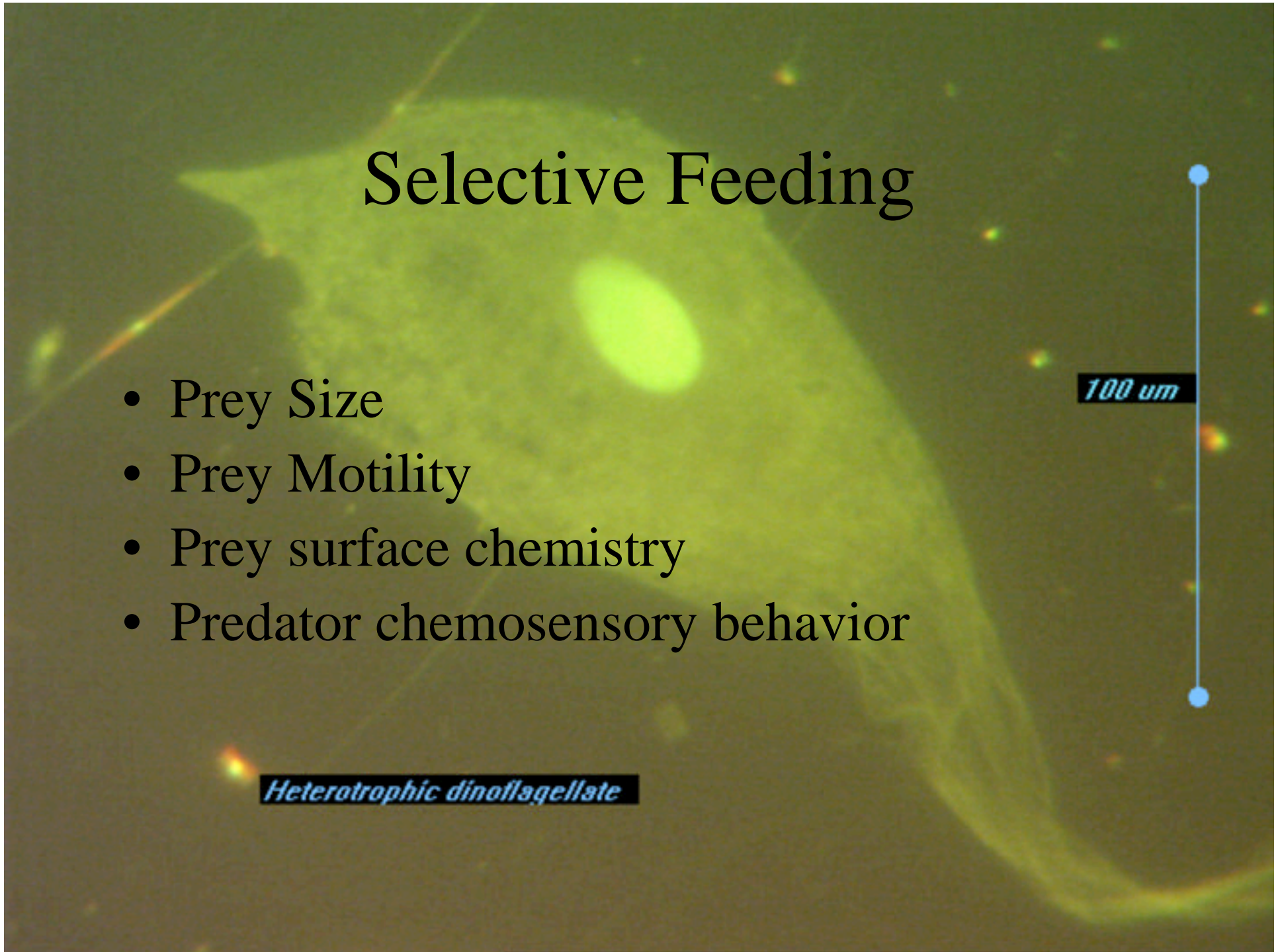
Comparison of day and night net tow profiles for (a) *Euphausia hemigibba*, a vertically migrating euphausiid, and (b) *Nyctiphanes simplex*, a non-migrating euphausiid that avoids nets during daylight, at stations in the California Current. Numbers beside the curves are vertical integrals (number m⁻²). Brinton 1967a.

Selective Feeding

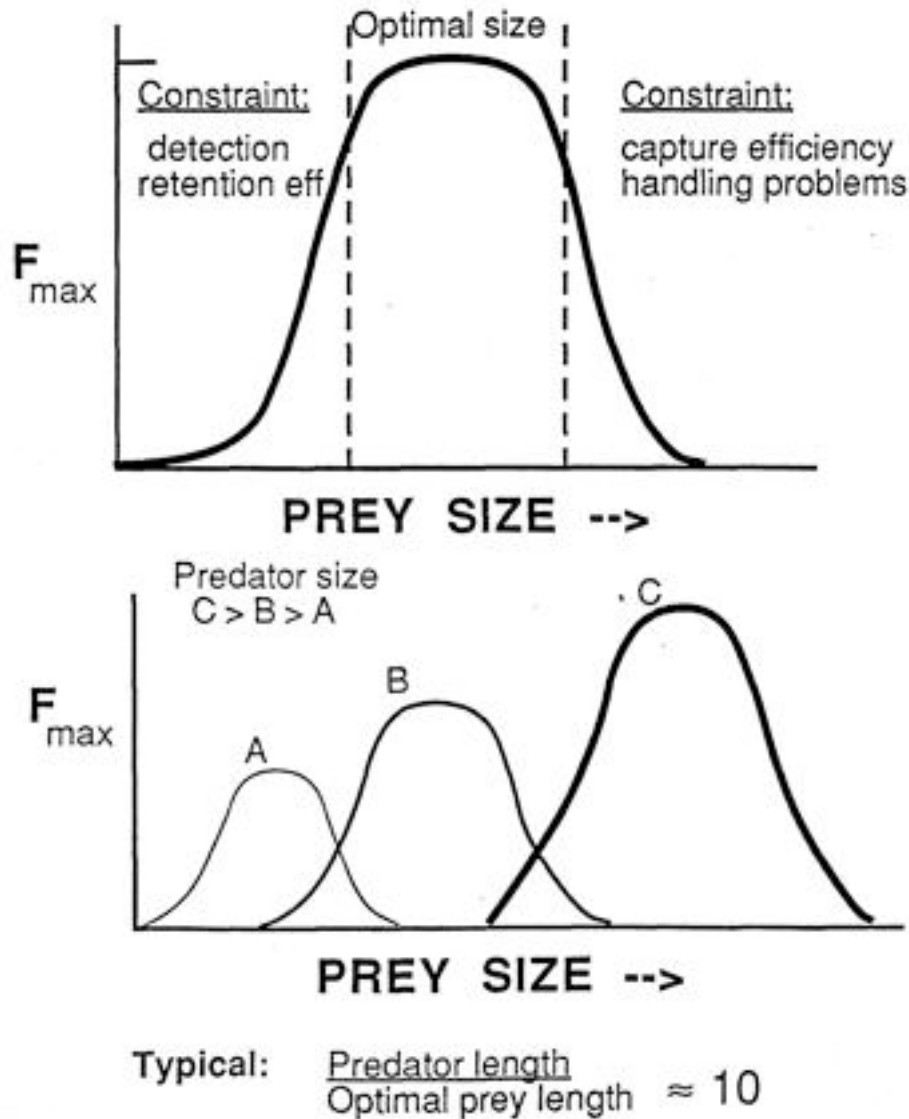
- Prey Size
- Prey Motility
- Prey surface chemistry
- Predator chemosensory behavior

100 μm

Heterotrophic dinoflagellate



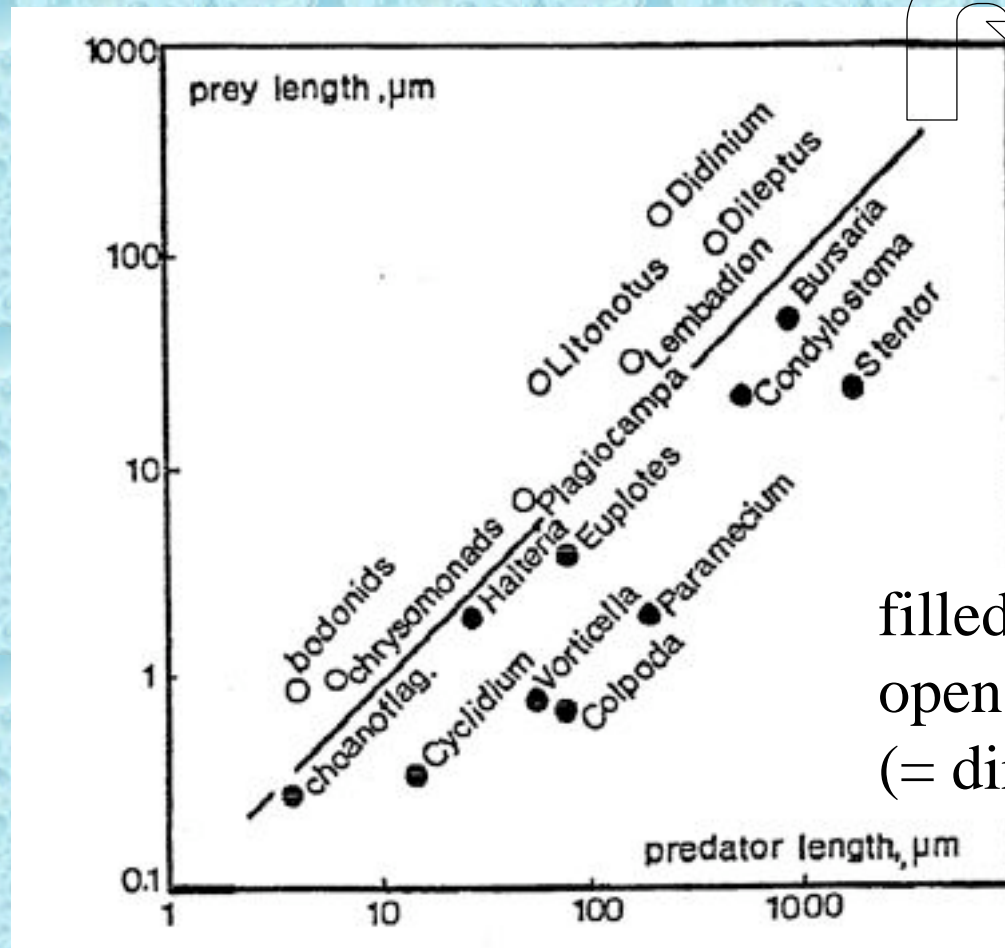
Prey:Predator Size Ratios



All organisms feed selectively, the optimal range of prey being determined by:

- Sensory mechanisms & thresholds for detecting prey
- Physical constraints on contact (encounter) frequency
- Minimum size that can be effectively captured/handled
- Maximum size that can be effectively captured/handled

Food particle size as a function of predator size: Protist examples



line = 1:10 food:predator size

filled circles: filter feeders
open circles: raptorial feeders
(= direct interception feeders)

Fenchel 1986

Protist optimum prey Selection: Is it 10:1?

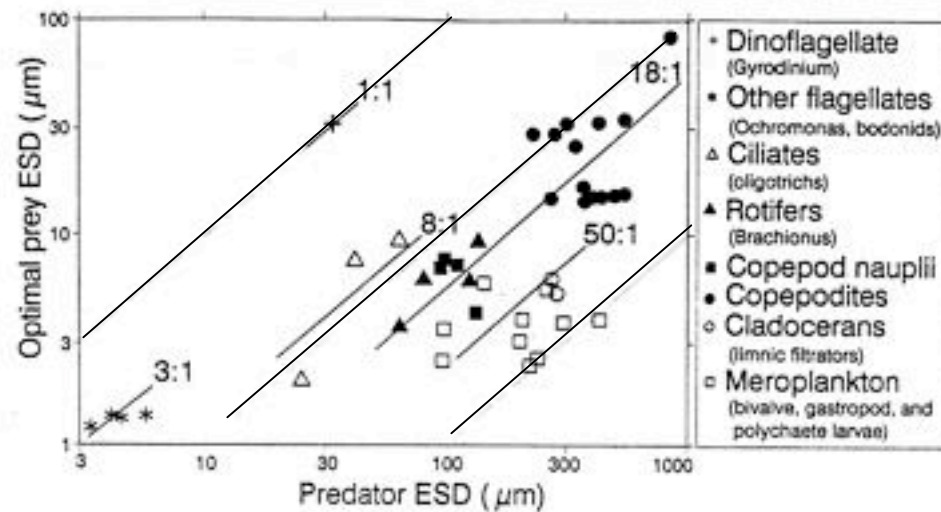


Fig. 2. Optimum prey size vs. predator size, both expressed as equivalent spherical diameter (ESD), data from Table 1. Lines represent average predator:prey size ratios for different groups of organisms (cf. Table 2).

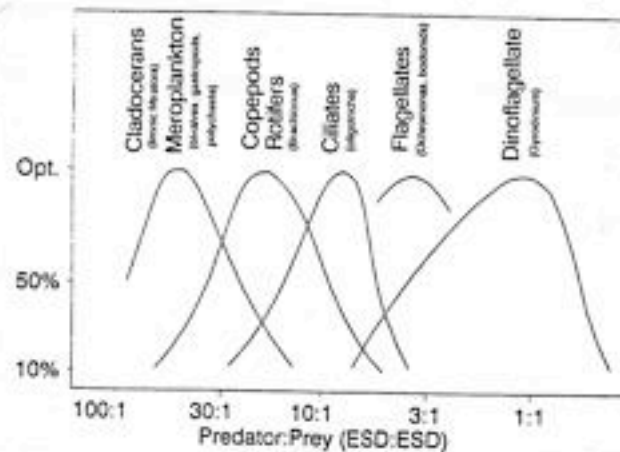


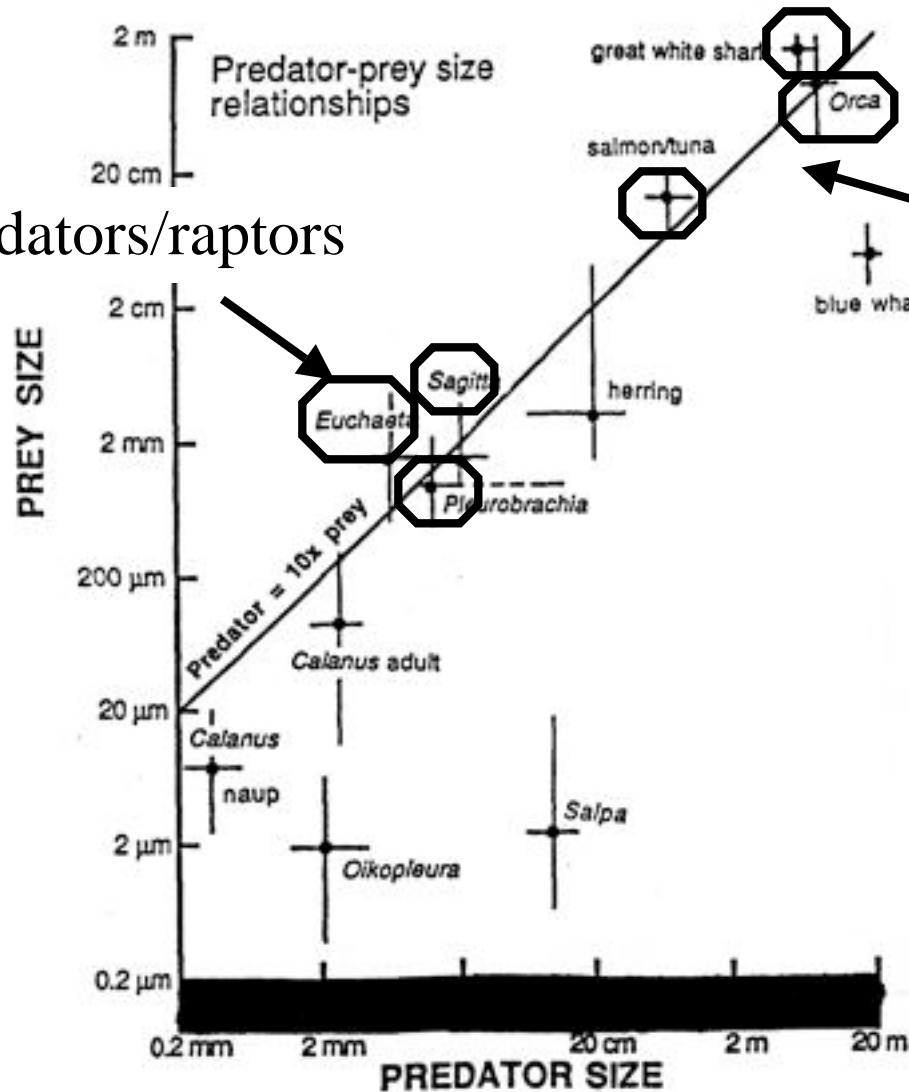
Fig. 3. Provisional size selectivity spectra for different pelagic predators based on information in Tables 1 and 2.

Metazoan Predators

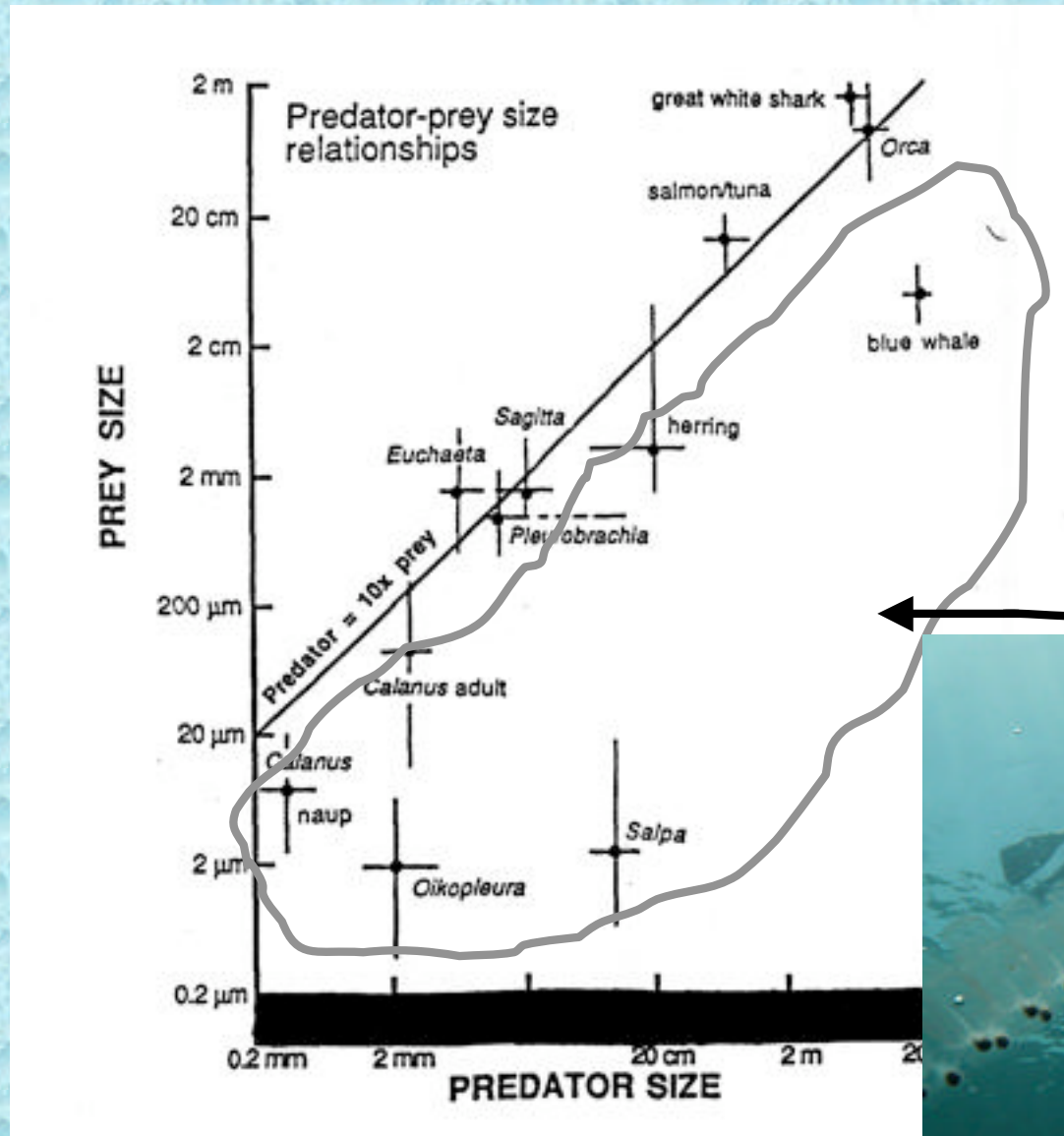
Raptors above the 1:10 line

ambush predators/raptors

raptorial feeders



Filter feeders below 1:10 line



filter feeders



wikipedia entry

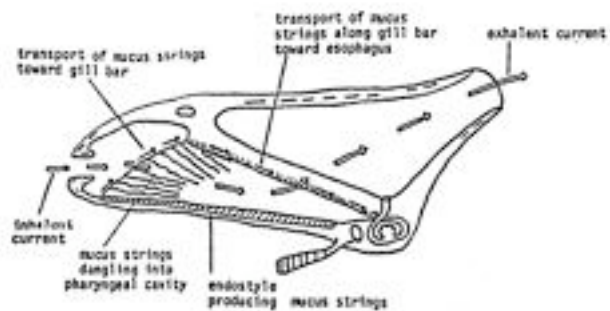
Appendicularians (Hemichordata)

ex. *Oikopleura*

Potentially important as
grazers of picoplankton

e.g., episodically responsible
for removing 50-60% of
standing stock daily in K.
Bay (Scheinberg dissert.)

Feeding currents in a salp



Reprinted from *J. Zool., Lond.* (1977) 181, 173-188

Howe morphology and mechanisms of feeding in the Oikopleuridae (Tunicata, Appendicularia)

ALICE L. ALLOREDGE*

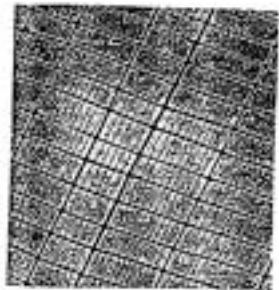
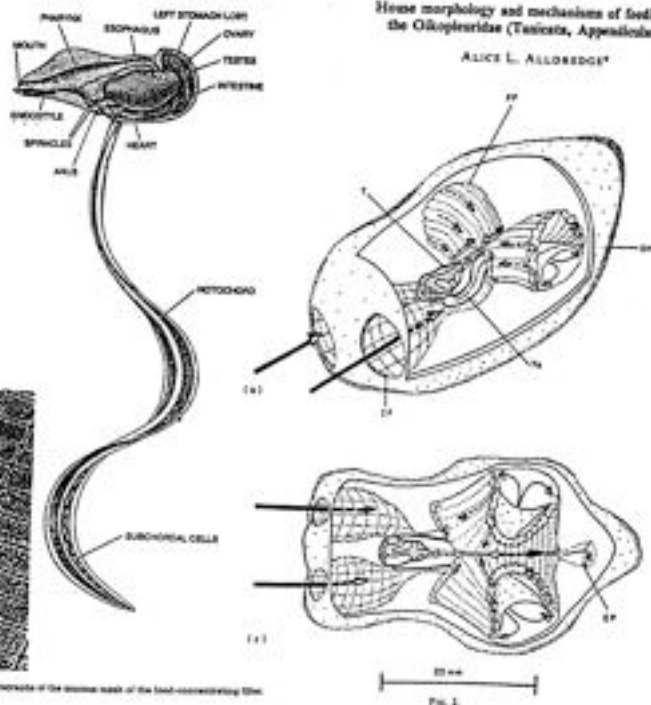


Fig. 1. *Oikopleura* *oikopleura*. Transmission electron micrograph of the tunic mesh of the food-collecting filter.

Copepod Size Selection

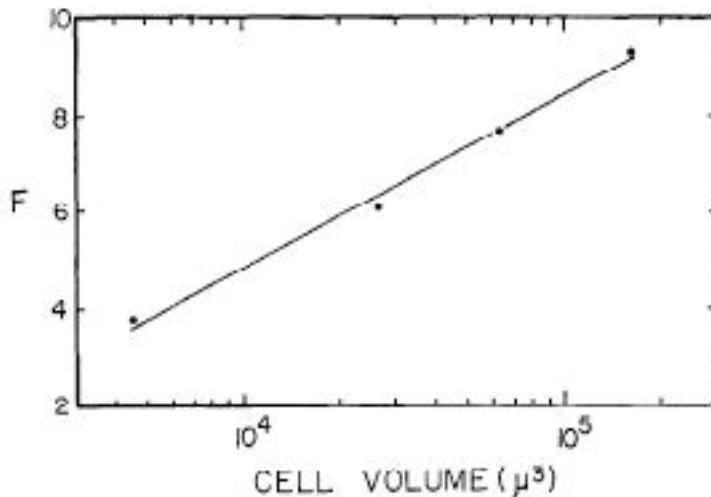


FIG. 5. Relationship between volume swept clear, F , for adult females of *Calanus* and mean cell volume of diatoms used as food. Values of F are means based on rates measured at cell densities below the critical concentration for each species of diatom (Figs. 2 and 4). F is predicted by the least-squares regression line $F = 2.61(\log V) - 4.84$, where V is the cell volume (μ^3) of the centric diatom used as food. The correlation coefficient between $\log V$ and F is 0.79 ($N = 95$).

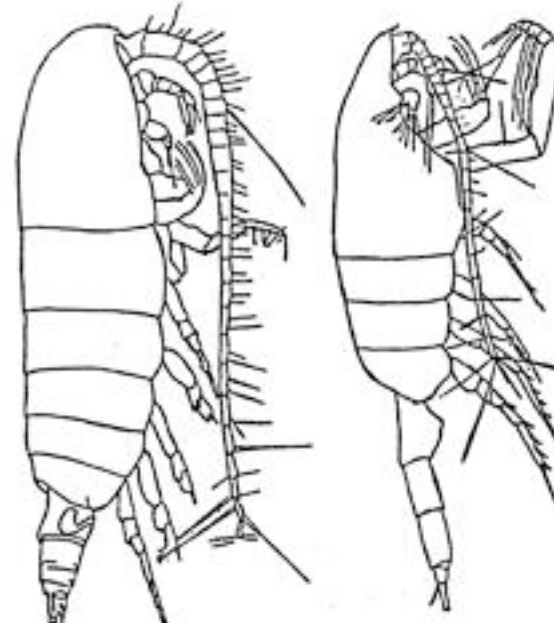
Calanus pacificus:
higher clearance rates on
larger prey items

Frost 1972

Crustacean feeding appendages

filter feeder:
crushing mandible,
fine hairs on appendages

predator:
slicing mandible,
no hairs on appendages

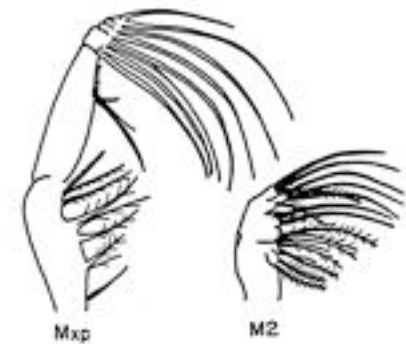
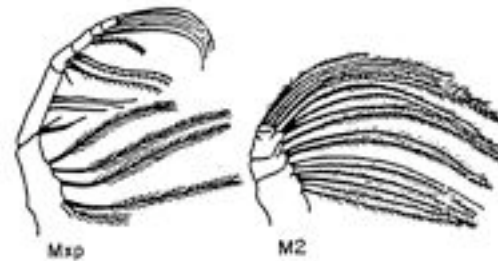


Filter feeder

Predator



Cutting edge
of mandible



Why some don't feed on small organisms

Herbivorous copepod, *Acartia clausi*

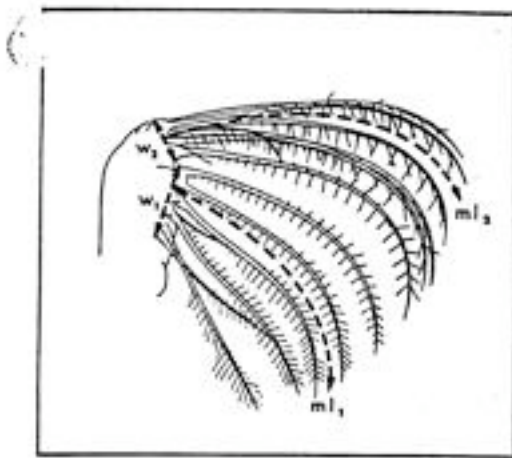


Fig. 1. Maxilla of adult female *Acartia clausi* (drawn after a photograph of a mounted limb) showing the position of the setules on the setae and the way the measurements were made for surface calculations. w = width of the small (w_s) and large (w_l) meshed region; ml = mean length of the setae of the small (ml_s) and large (ml_l) meshed region.

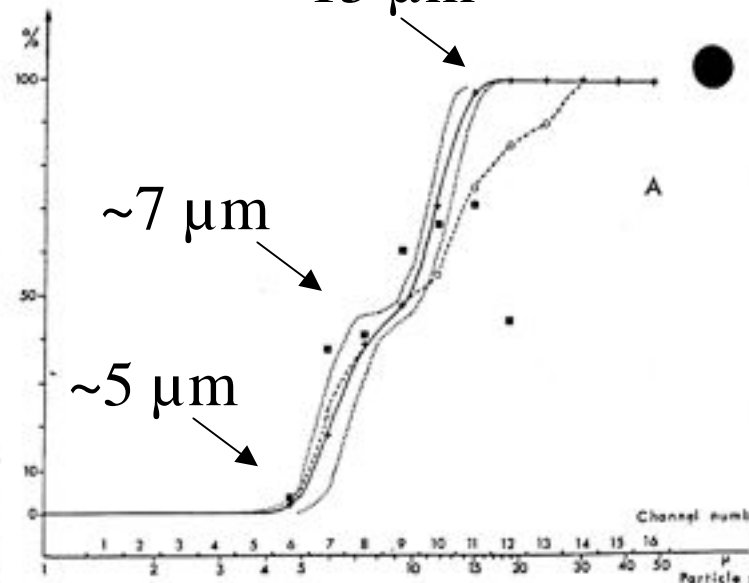


Fig. 3. Spectra of filtration efficiency (computed from the measurements of setae) for each developmental stage of *Acartia clausi*. Each line represents the spectrum of one animal; curves were interrupted as soon as 100% efficiency was reached.

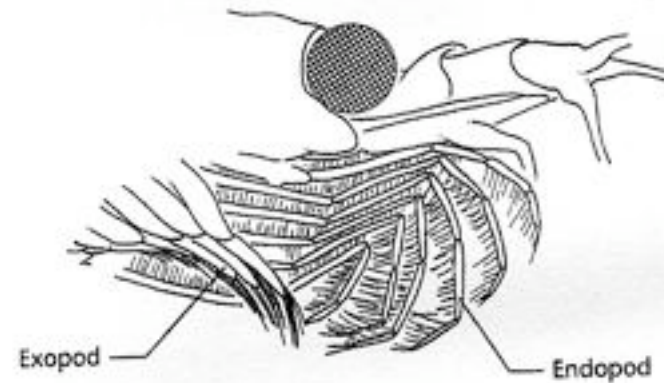
Nival & Nival 1976

Crustaceans that CAN capture small prey

e.g., euphausiid feeding
appendages



(a)



(b)

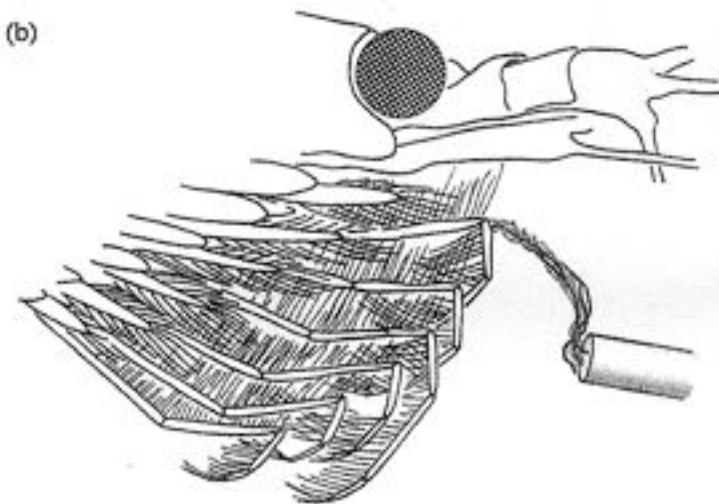


Fig. 7.2 Thoracic legs of particle-feeding euphausiids bear long anteriorly directed setae forming a filter basket (closed in a). This fills from the front, beneath the antennae, when the legs are opened (b; flow is shown by the dye stream moving from a pipette tip at the right). During opening the filter surface is covered by the exopods (outer legs) to keep water from moving in through the screen. (After Hamner 1988.)

Copepod diets vs. Ambient food availability

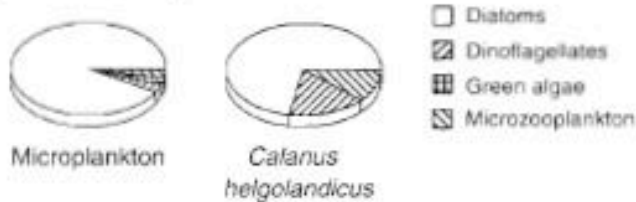
(a) Central California, Aug. 2, 1987 – Diatom bloom at front



(e) Los Angeles Harbor, Nov. 1986 to Oct. 1987 (mean of 10 expts)



(b) Irish Sea, May 3, 1989



(f) Los Angeles Harbor, Apr. 1987 – Dinoflagellate bloom



(c) Irish Sea, May 2, 1989



(g) Los Angeles Harbor, Feb. 1987 – Low production period



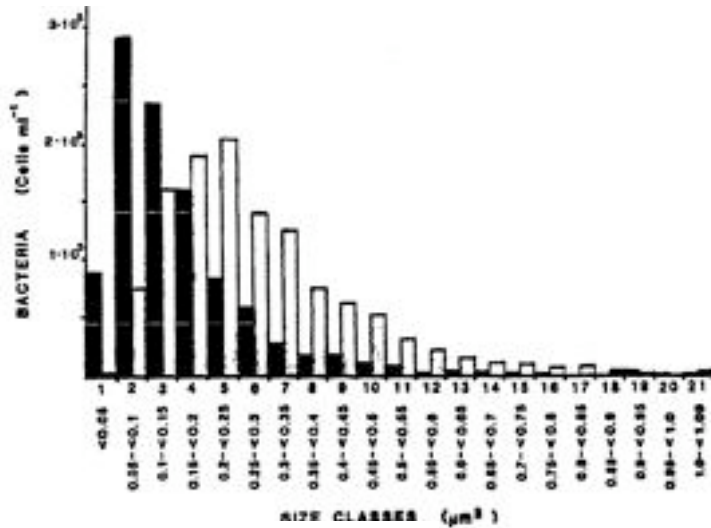
(d) NE Gulf of Mexico, Mar. 21, 1992



(h) NE Gulf of Mexico, Mar. 21, 1992



Heterotrophic flagellate feeding on bacteria



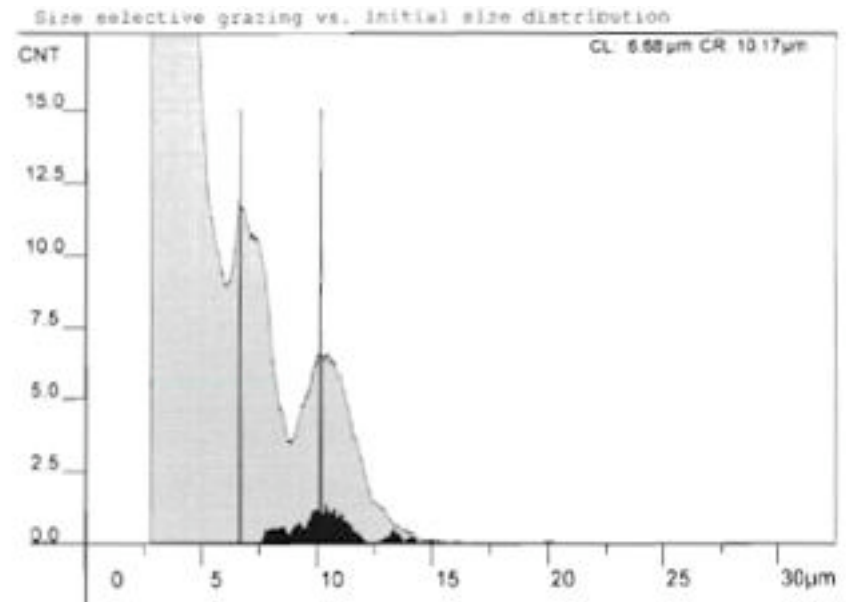
Andersson et al. 1986

Microzooplankton Size Selection

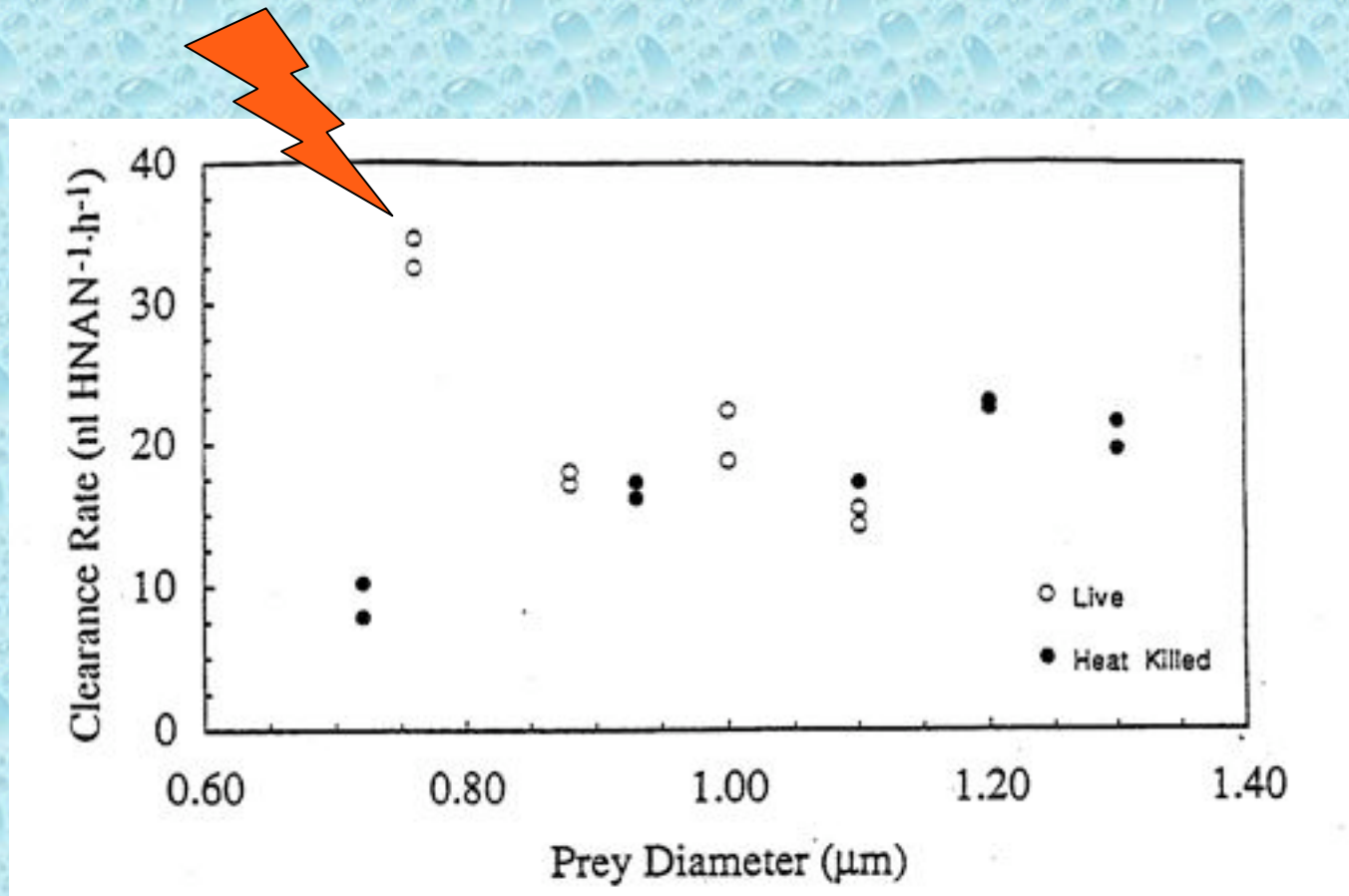
Weisse & Kirchhoff 1997

Fig. 8. Size-selective grazing of *Peridiniopsis berolinense* (dark shaded area) versus the initial algal size distribution (light shaded area) measured by EPCS in the first experiment. The y-axis denotes count rate, i.e. number of particles per each of the 1024 channels of the equivalent spherical diameter (ESD, x-axis); the latter is a measure of cell size. The dark area thus indicates the size range where feeding was effective and the number of algae in each channel that have been grazed during the experiment. Cursors mark the abundance peak of *Rhodomonas minuta* (left) and *Cryptomonas* sp. (right), respectively. The corresponding ESD are given in the top right corner (CL: cursor left, *R. minuta*; CR: cursor right, *Cryptomonas* sp.)

Dinoflagellate feeding on algae

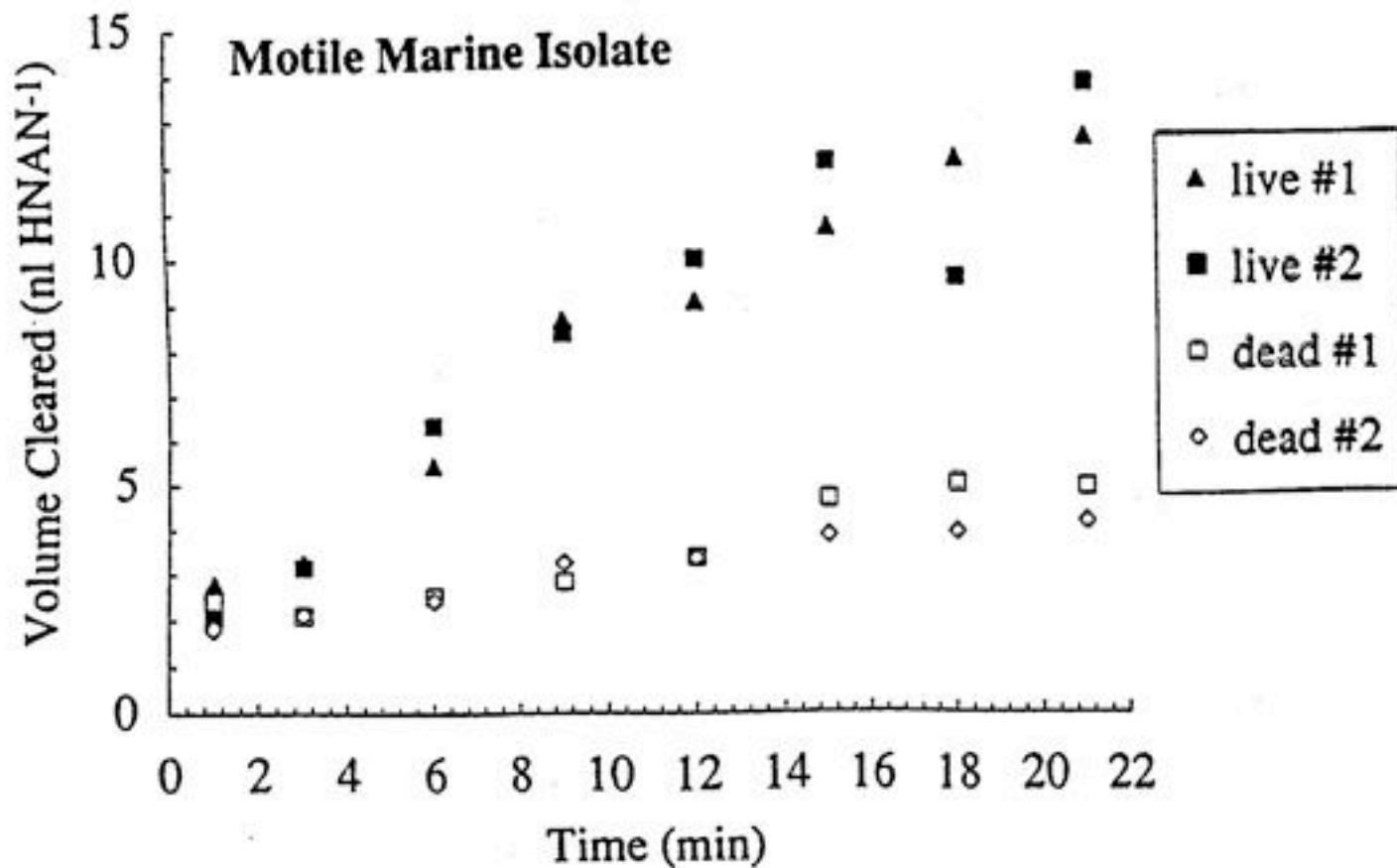


Selection based on Prey Size



Monger & Landry 1992

Motility of Prey



Uptake of fluorescently-labelled, living and heat-killed cultures of a highly motile marine bacteria (Kaneohe Bay isolate) by the flagellate HNAN.

Monger & Landry 1992

Prey motility a factor for other predators?

Cruising (swimming) predators:

Swimming prey will increase encounter rates

Ambush (sit-and-wait) predators:

Predators that detect prey motion (vibrations) will clearly detect more motile prey

Chaetognaths (arrow worms)

e.g., *Sagitta*

- Ambush predators, mainly feed on copepods
- Common, 1 - 10 cm long
- Sensory hairs to detect vibrations of prey
- Once prey captured, it is injected with a neurotoxin



Some predators switch between one behavior and another to optimize energy intake

Centropages: ciliates preferred as prey if over 5% of the mixture

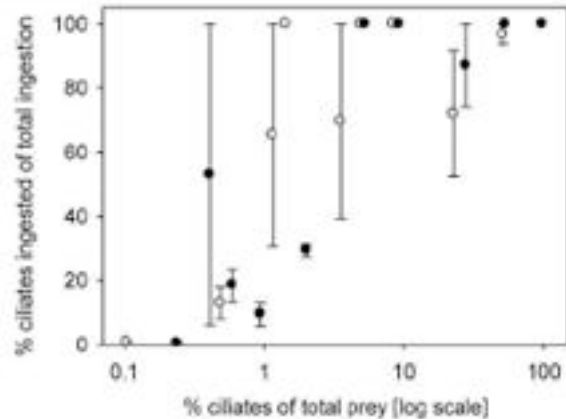


Fig. 3. *Centropages hamatus*. Feeding of males (m; filled) and females (f; open) on ciliates when offered a mixture of *Rimostrombidium caudatum* and *Thalassiosira weissflogii* (see Section 2 for details). Error bars indicate mean \pm standard error.

Saage et al. 2009



www.arcodiv.org

www.zooplankton-online.net

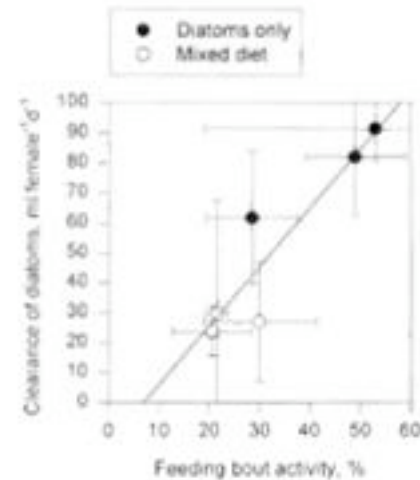
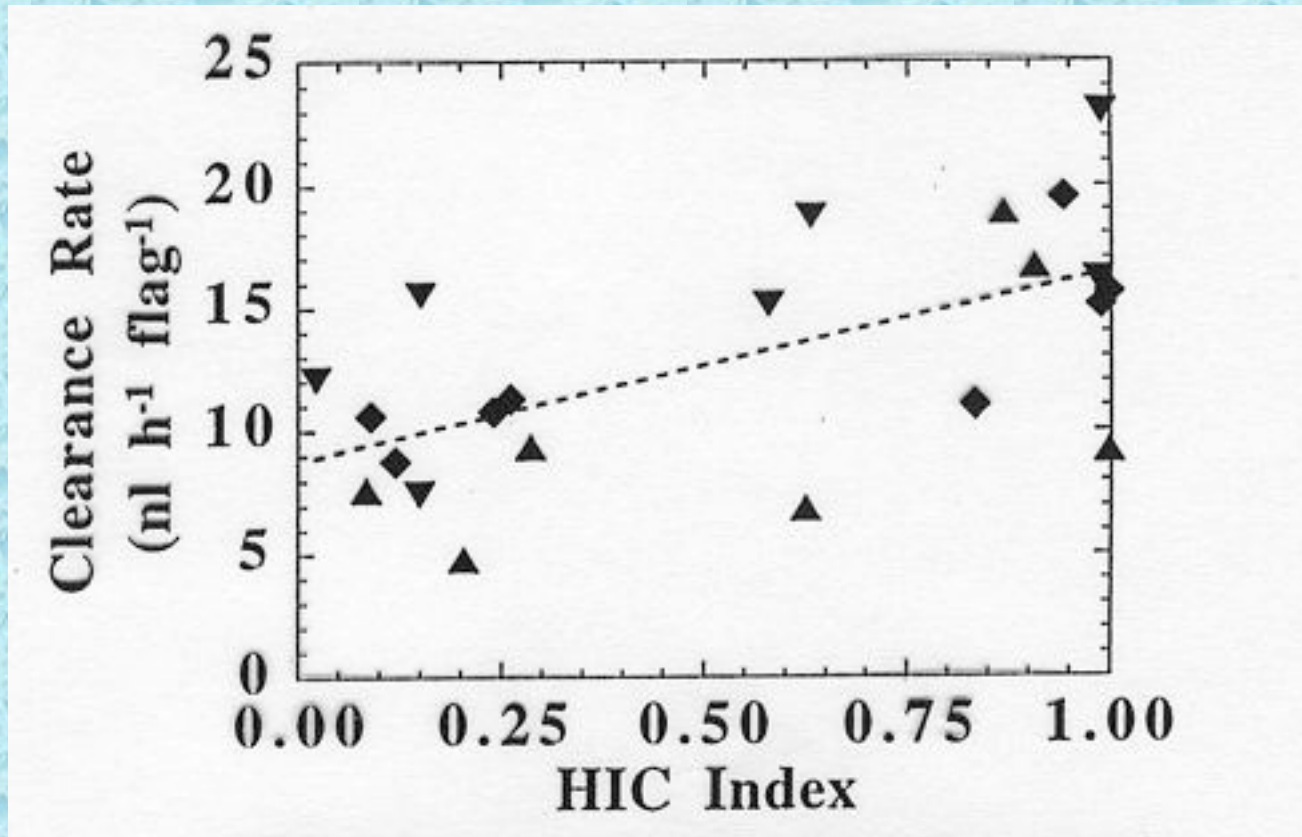


Fig. 4. *Acartia tonsa*. Clearance rate of diatoms by *A. tonsa* as a function of feeding bout activity: (O) mixture of diatom *Thalassiosira weissflogii* and ciliate *Strombidium sulcatum*; (●) *T. weissflogii* only. Feeding bout activity and clearance were measured in separate experiments conducted simultaneously. The regression is statistically significant ($n = 6$, $r^2 = 0.84$, $p < 5\%$). Error bars show \pm SD.

Kiorboe et al. 1996

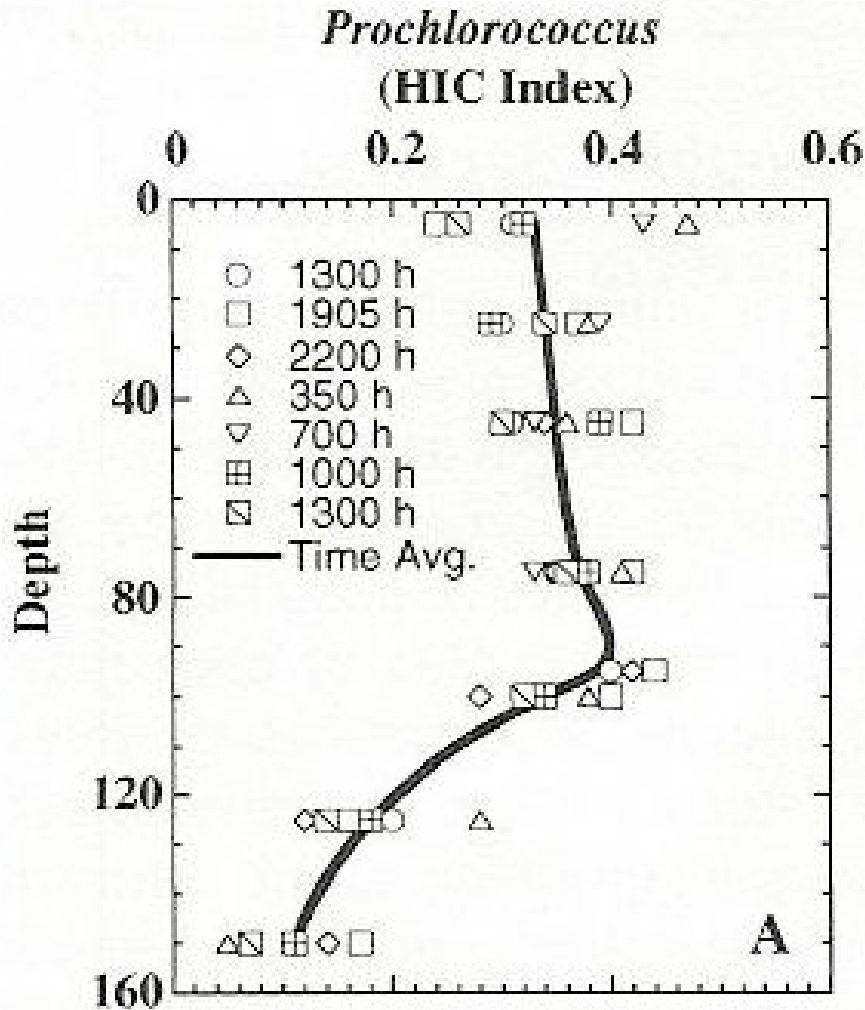
Acartia tonsa feeding on diatoms vs. ciliates

Prey Hydrophobicity (surface chemistry)



Monger et al. 1999

Hydrophobicity of *Prochlorococcus*

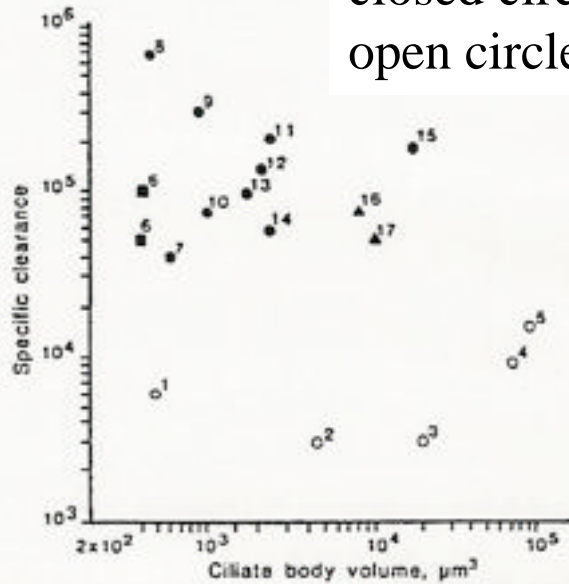


Why the difference?

- 1) genetic?
- 2) nutrient starvation response: attach to surfaces?
- 3) Growth limited by a hydrophobic compound?

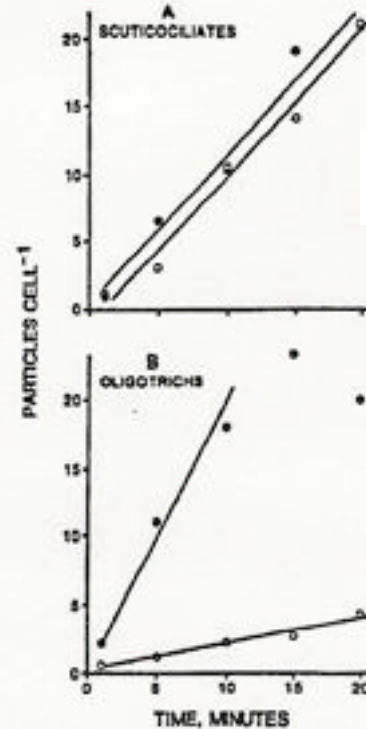
Chemosensory Behavior in Protists?

closed circles: FLB
open circles: latex beads



Fenchel 1980 &
Sherr & Sherr 1987

(1987)

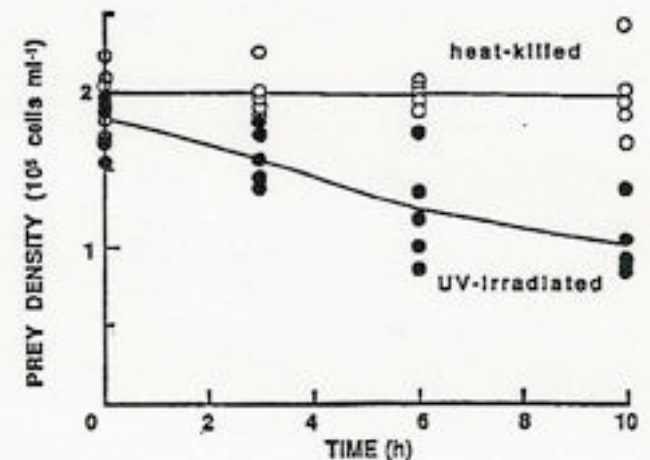


closed circles: FLB
open circles: microspheres

ciliate w/fixed filter apparatus

ciliate w/membranelle filter

Sherr et al. 1987



Landry et al. 1991

Pallium Feeding

- Preferred diatoms over dinoflagellate prey
- Appeared to respond to chemosensory cues
- Had greater capture success with non-motile prey

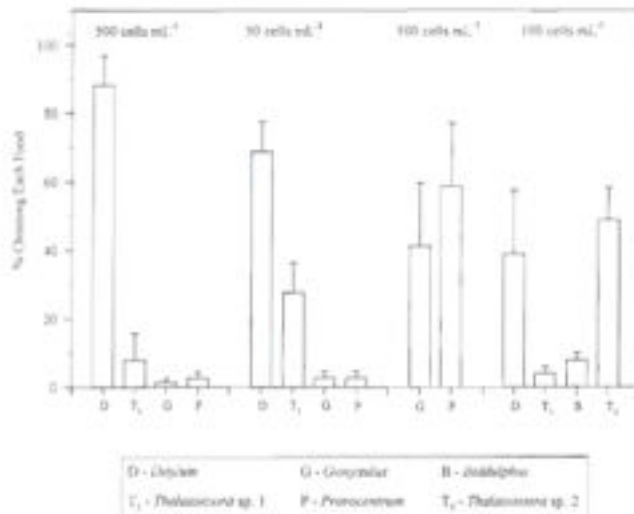


Fig. 3. *Protoperidinium pellicudum* Feeding selectivity studies. Percent of the time that each of 4 phytoplankton foods (*Ditylum brightwellii*, *Thalassiosira* sp. 1, *Gonyaulax polyedra* or *Prorocentrum micans*) were chosen at food concentrations of 500 cells ml^{-1} or 50 cells ml^{-1} of each food, that each of 2 dinoflagellate species were chosen at 500 cells ml^{-1} , or that each of 4 diatom species (*Ditylum brightwellii*, *Thalassiosira* sp. 1, *Biddulphia* sp. or *Thalassiosira* sp. 2) were chosen at 100 cells ml^{-1} .

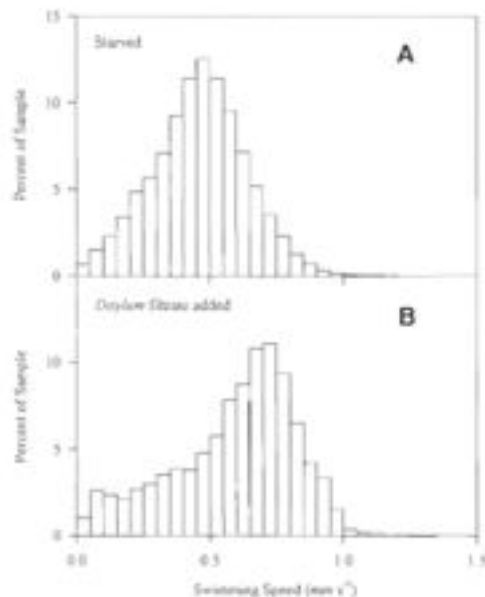


Fig. 5. *Protoperidinium pellicudum* Distribution of swimming speeds (A) after ca 20 h of starvation and (B) after having been exposed to a fresh filtrate from a culture of actively growing *Ditylum brightwellii*.

Table 2. Observed feeding interactions between *Protoperidinium pellicudum* and 4 potential food types: *Ditylum brightwellii*, *Thalassiosira* sp. 1, *Gonyaulax polyedra* and *Prorocentrum micans*. If *P. pellicudum* formed a pallium around its food cell, it was scored as a successful capture. If the cell was lost after the tow thread was attached, it was scored as an escape. If *P. pellicudum* circled the cell in a stereotypical feeding behavior, but failed to attach a tow thread, it was scored as a lost contact. n = no. of observations

Prey	Prey speed (mm s^{-1})	Successful capture	Escape	Lost contact	n
<i>Ditylum brightwellii</i>	0	100%	0	0	115
<i>Thalassiosira</i> sp. 1	0	98.3%	1.7%	0	116
<i>Gonyaulax polyedra</i>	0.4	61.9%	21.2%	16.9%	118
<i>Prorocentrum micans</i>	0.1	46%	43%	11%	100

Buskey 1997

- Higher growth rate on diatoms (0.7 d^{-1}) vs. dinoflagellates (0.4 d^{-1})

Copepod Selective Feeding: toxic and non-toxic dinoflagellate

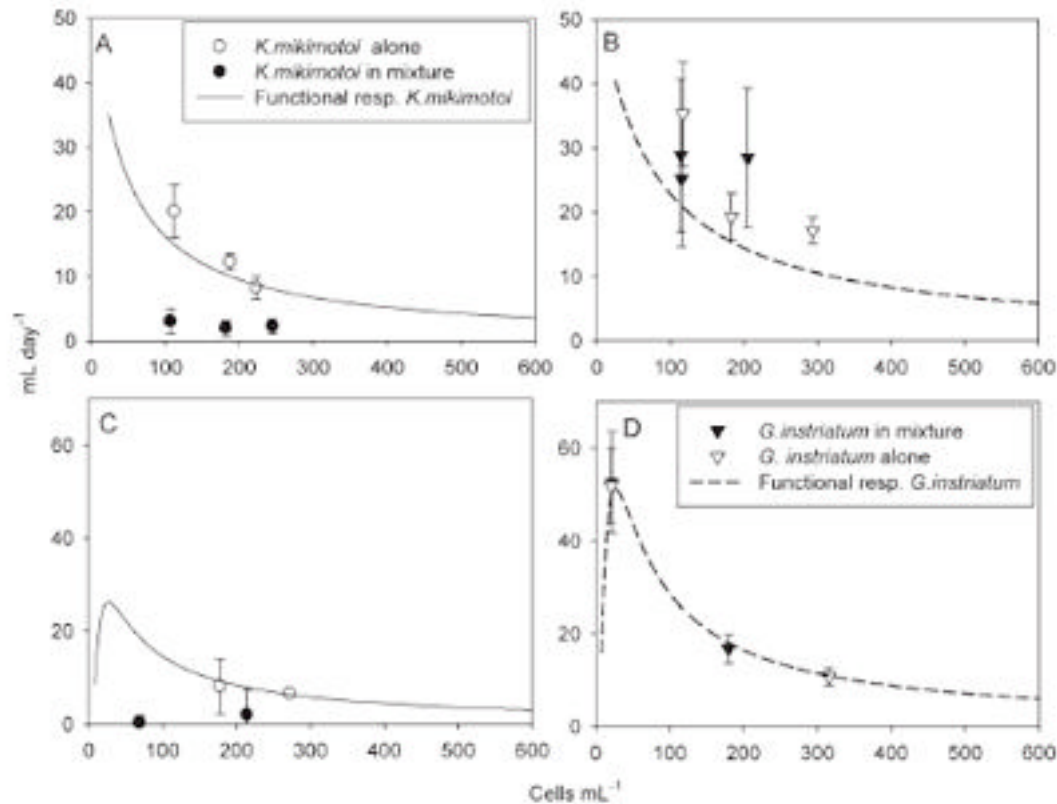
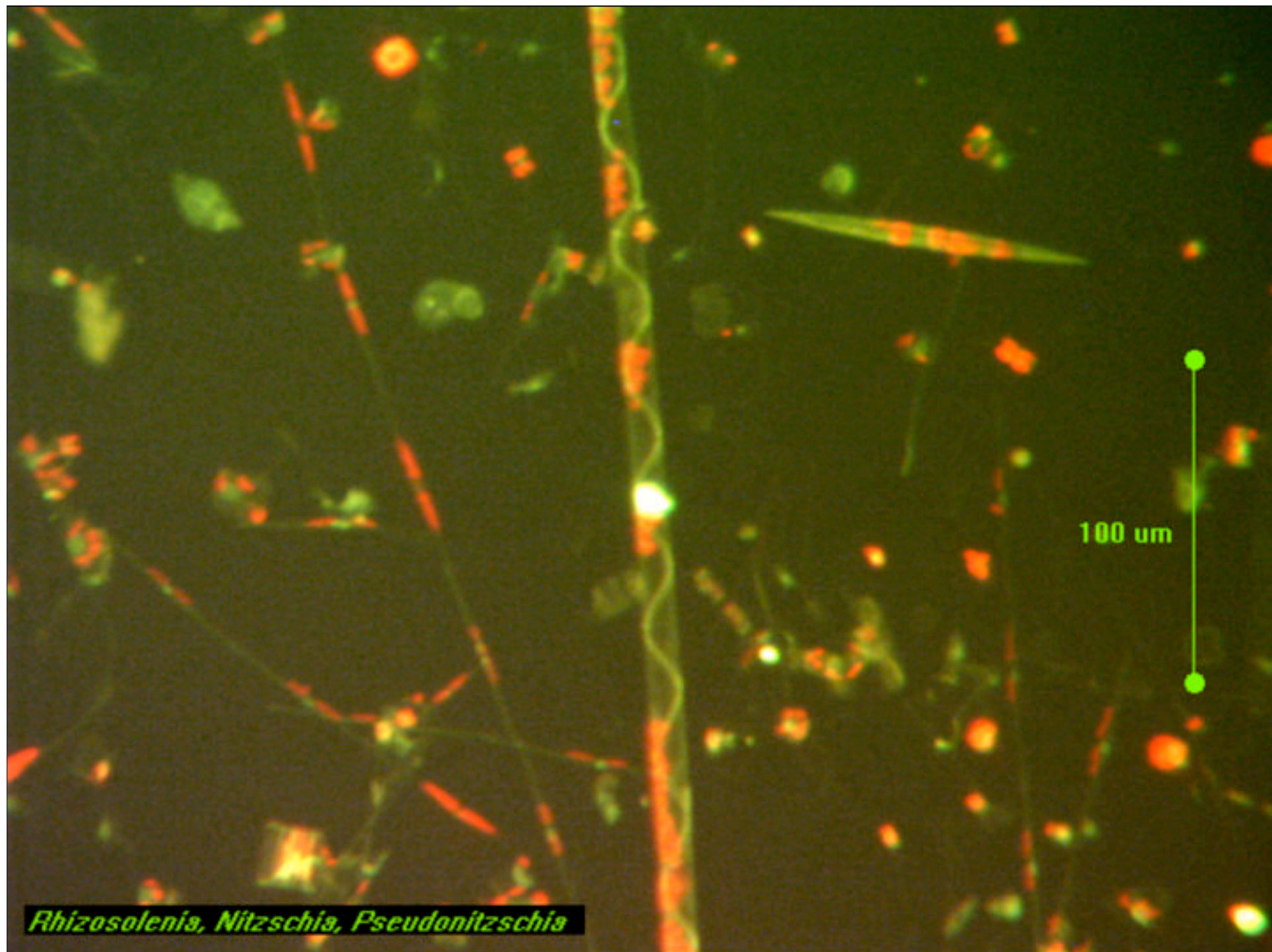


Fig. 3. Clearance rate of *Pseudocyclops elongatus* on *Karenia mikimotoi* (A) and *Gyrodinium aureolum* (B), and clearance rate of *Temora longicornis* on *K. mikimotoi* (C) and *Gyrodinium aureolum* (D) when presented alone (open symbols) or in a mixture (closed symbols). For comparison, the functional response curves from the single-prey species experiments in Fig. 1 are shown (the lines). Vertical bars show standard deviation.

When offered
both prey types,
fed more on non-
toxic species

Prey rejection
frequencies same
between mono and
mixed diets: suggests
remote sensing
(chemosensis) of cells



Rhizosolenia, Nitzschia, Pseudonitzschia