ZOOPLANKTON GRAZING: CAPTURING FOOD AT LOW RE

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Assignment

Topics

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   b. What are Holling Type 1, Type 2, and Type 3 functional response curves (**Holling 1959**)?
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REQUIRED READING

Koehl, M. A. R. and J. R. Strickler. 1981. Copepod feeding currents: food capture at low Reynold's number. Limnol. Oceanogr. *26*: 1062-1073. *[The paper that changed the way people analyzed copepod grazing.]*

Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. [*Read Chapter 7 pp. 129-146 on zooplankton grazing. Skim Chapter 6, an overview of zooplankton]*

SUPPLEMENTAL

Båmstedt, U., D. J. Gifford, X. Irigoien, A. Atkinson, and M. Roman. 2000. Feeding. Pp. 297-399 *in* R. Harris, P. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley, eds., ICES Zooplankton Methodology Manual. Academic Press, San Diego. 684 pp. *[This is the best available compilation of methods]*

Banse, K. 1992. Grazing, temporal changes of phytoplankton concentrations, & the microbial loop in the open sea. Pp. 409-440 *in* P. G. Falkowski & A. D. Woodhead, *eds*., Primary Productivity & Biogeochemical Cycles in the Sea. Plenum Press, New York. *[An excellent review of the global importance of zooplankton grazing & nutrient regeneration. Banse divides the ocean into 3 domains. The 1st domain includes the so-called oligotrophic gyres, the second the High Nutrient Low Chlorophyll a zones (e. g., Station P), & the 3rd domain includes the classic N. Atlantic bloom region. Banse points out the central importance of grazing & nutrient regeneration in all three zones & illustrates his arguments with estimates of the relative importance of grazing to the other terms in the advection-diffusion-growth model of phytoplankton]*

Frost, B. W. 1980. Grazing. Pp. 465-491 *in* I. Morris, ed., The Physiological ecology of phytoplankton. Blackwell's, Edinburgh. *[Frost reviews the basics of zooplankton ingestion and demonstrates the importance of zooplankton grazing using ecosystem simulation models (modified from John Steele's North Sea model).]*

Purcell, A. M. 1977. Life at low Reynolds number. Am. J. Physics. *45*: 3-11.

Price, H. J. 1988. Feeding mechanisms in marine and freshwater zooplankton. Bull. Mar. Sci. *43*: 327-343. *[A brief review of the mechanisms by which zooplankton detect, pursue and ingest their prey.]*

Welschmeyer, N. A. and C. J. Lorenzen. 1985. Chlorophyll budgets: zooplankton grazing and phytoplankton growth in a temperate fjord and the Central Pacific gyre. Limnol. Oceanogr. *30*: 1-21. *[Following Shuman's discovery that Chl a is stoichiometrically converted to pheophorbide a in copepod guts, W & S balance the water-column grazing budget, calculating the relative importance of macro- and microzooplankton grazing.]*

Comments on grazing

INTRODUCTION

Just as there are many methods to estimate primary production, there are many techniques used to estimate the grazing rates of zooplankton on phytoplankton in the laboratory and the field. The two required papers view zooplankton grazing from the micron scale (**Koehl & Strickler 1981)** to the global (**Banse 1992**). **Frost (1980)**, on the supplemental listing, provides a general introduction to why grazing is important, even to non-zooplankton ecologists. Frost at the University of Washington and Paffenhöfer (*e. g.*, **1971**, **1988**, **Paffenhöfer & Stearns 1988**,

Paffenhöfer & Lewis 1990) at the Skidaway Institute of Oceanography led the way in estimating grazing rates of calanoid copepods and modeling the implications of their feeding. Both **Banse (1992)** and **Frost (1980)** describe the role of grazing in ecosystem models of the plankton. Frost discusses some effects of zooplankton grazing on phytoplankton and then modifies Steele's North Sea model to model the effects of grazing in temperate and oligotrophic waters. By the way, you can download this model from my web page (**http://www. es. umb. edu/edgwebp. htm**) and run it DOS-based PC's. I can provide copies on a diskette as well.

Frost (1980) was written at the time one major change was occurring and a second major change in our understanding was on the way. The first major change was the discovery of the importance of small-scale hydrodynamics on zooplankton feeding. The second major advance was the finding that macrozooplankton, the subjects of much of Frost and Paffenhöfer's work, were less important grazers in most of the world's ocean than the microzooplankton. Microzooplankton, the size of ciliates (≈ 10-40µm in size) may be the major grazers of phytoplankton (Fenchel **1980**, **1988**, **Azam et al. 1983**, **Stoecker et al. 1986**, **Waterhouse & Welschmeyer 1995**). **Koehl & Strickler (1981)** is the key paper refuting the idea that copepods feed using a leaky sieve. The leaky-sieve hypothesis was proposed by **Nival & Nival (1973)** and **Boyd (1976)** to account for the greater ingestion efficiency for large cells by copepods. **Frost (1977)** provides a concise review of this hypothesis and evidence that supports it. The leaky-sieve hypothesis states that the brushy 2nd maxillae of calanoid copepods acts as a sieve, with a variety of sizes of sieve openings. This hypothesis predicts that larger phytoplankton cells are trapped efficiently as water is moved through the sieve-like 2nd maxillae, but a significant fraction of small cells could pass through the larger intersetule openings. **Koehl & Strickler (1981)** argue persuasively that the 2nd maxillae could not act as a sieve, and propose a more likely explanation for the higher selectively for large cells: they are more likely to be detected by the chemoreceptors used by copepods and other large grazers.

Banse (1992) used satellite remote sensing data to divide the oceans into three zones based on the seasonal change of Chl *a*. He provides an historical perspective on why grazing wasn't emphasized sufficiently as a major factor controlling the global distribution of Chl *a*. He urges more use of ecosystem simulation models, in which grazing plays a prominent role.

Welschmeyer & Lorenzen (1985), on the supplemental reference list, describe an innovative approach for estimating the relative importance of macrozooplankton grazing in two different marine environments. **Welschmeyer & Lorenzen (1985)** show how the downward flux of pheophorbide *a*, produced as Chl *a* passes through the gut of a grazer, can be used to estimate the relative importance of micro- and macrozooplankton grazing.

THE REFUTED LEAKY-SIEVE HYPOTHESIS

The hypothesis

The old view of copepod feeding was that calanoid copepods filtered phytoplankton with "a leaky sieve" (**Nival & Nival 1973**, **Boyd 1976**). This was consistent with diagrams of the feeding currents around copepods that appeared to show that fluid moved through stationary 2nd

maxillae (see **Koehl & Strickler 1981** Fig. 1B). The filtration efficiency of zooplankton on different sizes of phytoplankton was believed to be controlled by the intersetule spacing. Calanoid copepods were even thought to adjust the intersetule spacing in relation to the modal size of phytoplankton to maximize the capture efficiency of phytoplankton cells.

The refutation: Life at low Re

The high-speed cinematography of Rudy Strickler and co-workers has largely ended the lengthy debate over the "leaky-sieve" hypothesis. They document that calanoid copepod feeding is a low Reynolds number phenomenon. The Reynolds number is a dimensionless number:

$$
\begin{aligned}
Re &= \frac{L\ v\ \rho}{\eta}, \quad or \\
&= \frac{L\ v}{\nu}. \\
where,\ L &= characteristic\ length\ scale\ [cm]. \\
v &= velocity \left[\frac{cm}{s}\right]. \\
\rho &= fluid\ density. \\
\nu &= nu = kinematic\ viscosity \left[\frac{cm^2}{s}\right]. \\
\eta &= eta = dynamic\ viscosity \left[\frac{g}{cm\ s}\right].
\end{aligned}
\tag{1}
$$

For seawater and freshwater (at 20°C), $\nu \approx 10^{-2} cm^2\ sec^{-1}$. For air at 20°C $\nu \approx 1.5 \times 10^{-5} cm^2\ sec^{-1}$.

At low Re, Re<<1, molecular viscosity and molecular diffusion dominate the transport of momentum and seawater properties. At high Re, Re>>1000, eddy diffusion dominates the transfer of momentum and seawater properties. The Reynolds number can be used to scale a variety of processes. **Vogel (1981, p. 80)** estimates the Reynolds number for a golf ball driven down the fairway at 5×10^4-1.5×10^5, which is close to the Reynolds number for my body as I peddle my bike ($\approx 10^5$). The Reynolds number is the centerpiece of fluid mechanics, or as **Vogel (1981, p. 65)** states:

> *"For a biologist, dealing with systems of an enormous size range, the Reynolds number is the central scaling parameter which makes order of a diverse set of physical phenomena. Its role is comparable to that of a surface-to-volume ratio in physiology. "*

A low Re means that viscous forces dominate over inertial forces; there is little turbulence and diffusive transport is controlled by molecular diffusive transport. **Purcell (1977)** discusses the counter-intuitive world of physics at low Re, a world in which bacteria use propellers to swim, molecular diffusion controls food supply, and despite the analogy that fluids are like molasses, swimming costs are nil.

Because of this low Re physics, copepods are suspension feeders but they cannot be regarded as filter feeders. Copepod feeding is a low Reynolds number phenomena. Copepod feeding is more like picking the crumbs from a honey bowl with a fork, rather than filtering leaves from a pool with a pump and filter. Picking crumbs from honey is difficult unless you spot the crumbs beforehand and do not have to filter much honey.

The mechanisms by which copepods detect and capture prey remains a very active area of research, reviewed by **Price (1988)**. Large zooplankton appear to feed by detecting the chemical plumes of individual large phytoplankton cells or chains of diatoms. Due to physics, large (>10 µm diameter) fast-growing cells should produce a relatively discrete plume of detectable dissolved organic matter around themselves. Small cells or slow growing cells will not produce only a small plume of dissolved organic matter. George Jackson (1987**a** & **b**) has shown that chemical detection is not a viable strategy for grazers feeding on small picoplankton-sized phytoplankton. Jackson modeled the rate of production and dissipation of dissolved organic matter around small cells. Phytoplankton cells less than 5 µm in size and heterotrophic bacteria do not produce a chemical plume that can be detected at a distance. Microzooplankton ingestion is still a low Re phenomenon, but detection of plumes at a distance does not work. These grazers may be "contact" feeders in that the cells must be almost in immediate contact with the grazer to be detected.

ESTIMATING GRAZING RATES

There are several approaches available for estimating the ingestion rates of zooplankton in the field. **Frost (1980)** briefly reviews most of these techniques:

In situ *methods*

- Direct estimates of changes in phytoplankton standing stocks with time. These data can be combined with estimates of autotrophic production rates (and other loss terms, *e. g.*, sinking) to produce an estimate of the total loss of phytoplankton due to grazing (both macrozooplankton and microzooplankton).
- Estimates of pheopigment flux into sediment traps (=particle interceptor collectors) [Shuman, **Welschmeyer & Lorenzen (1985)**, **Downs & Lorenzen (1985)**]. Calanoid copepods convert Chl *a* to pheophorbide *a* in their guts and produce fast-sinking fecal pellets. The flux of pheophorbide via fast-sinking pellets can be estimated by sediment traps. This pheophorbide flux can be converted to a water-column macrozooplankton grazing rate by assuming the C:Chl *a* ratio and the conversion efficiency of Chl *a* to Phe *a*.
- If estimates of primary production and daily change in phytoplankton standing stock are available, the rate of microzooplankton grazing can be determined by difference. Microzooplankton are operationally defined as anything that does not produce a fast-sinking fecal pellet. This approach has been criticized because pheopigments may be

degraded in zooplankton guts (**Conover *et al.* 1986**, **Head 1988**, **Lopez *et al.* 1988**, **Mayzaud & Razouls 1992**).

- Estimates of digestive enzyme activities (Poulet & Mayzaud's approach). P & M thought that the digestive enzyme activities should be positively correlated with ingestion rates. **Hassett & Landry (1990b)** showed this approach is badly flawed, and that digestive enzyme activity is most often negatively correlated with gut-clearance rate. **Head & Conover (1983)** and **Head *et al.* (1984)** used this technique.

Incubation methods

- The dilution method Direct estimates of changes in phytoplankton (and bacterial) standing stocks with time after dilution of the sample (**Landry & Hassett (1982)**, **Landry *et al.* (1995b)**, **Gallegos & Vant (1996)**). Zooplankton grazing rates are strongly density-dependent. Dilution of the sample reduces the zooplankton grazing rate, while leaving phytoplankton growth (relatively) unaffected. **Tremaine & Mills (1987)** analyze the assumptions of the dilution method. The dilution method can be combined with HPLC analysis of specific plant pigments to estimate the grazing rate on specific phytoplankton groups (**Burhill *et al.* 1987**, **Strom & Welschmeyer 1991**, **Waterhouse & Welschmeyer 1995**, **Latasa *et al.* 1997**).
- Grazer exclusion The quantitative importance of large grazers can sometimes be estimated by sieving out the larger organisms. Since microzooplankton overlap the phytoplankton in size, exclusion cannot be used to estimate microzooplankton grazing rates.

Species-specific methods

- Grazer enhancement experiments: Grazers can be added in known numbers to incubation chambers to estimate grazing rates.
- Estimates of copepod egg-production rates (which Checkley (1980) & Runge (1985) showed are directly related to feeding rate). Calanoid copepods can be isolated from the field and their egg production rate is analyzed for the following few hours. See also **Berggreen et al. (1988)**, Ohman (**1985a**, **1985b**)
- Estimates of gut fullness, usually estimated using gut fluorescence [**Mackas & Bohrer's (1976)** and Dagg's technique, also used by Head (**1986**, **1988**)]. The ingestion of algae and bacteria by ciliates can sometimes be estimated by visual inspection of feeding vacuoles. To estimate the grazing rate, one must also estimate the `contact time' (Peterson & Bradley), *i. e.*, the time during which the act of ingestion can be detected. **Murtaugh (1984)** presents some limitations. **Penry & Frost (1990)** present a strong critique of one of the major assumptions of the method: that egestion rate is a constant after copepods stop feeding. **Ohman (1988b)** applied the gut fullness method to California current copepods.

- Addition of tagged particles to a suspension of grazers. The tag may be either fluorescent or radioactive. Frost showed that ingestion rates of artificial particles are lower than on natural particles, and **Cowles *et al*. (1988)** used fluorescence-activated cell sorting to show that copepods can even distinguish between actively growing and senescent phytoplankton cells. **Rublee & Gallegos (1989)** used fluorescently labeled algae to estimate zooplankton ingestion rates.

Model-based methods

- Laboratory measurements of grazing rate (**GR**) as a function of phytoplankton concentration (**PH**). The change in phytoplankton concentration is usually monitored by Coulter counter. This hyperbolic **GR** vs. **PH** relationship can then be applied to the field to estimate the grazing rates. Estimates of the grazer and phytoplankton standing stocks are required.
- Comparison of laboratory and field development times can also reveal the extent of food limitation. **McLaren (1978)** argued that calanoid copepod field development times are closer to their temperature-determined optima. Therefore, copepods in general are not food-limited. **Ohman (1985a)** makes a similar argument for *Pseudocalanus* in Dabob Bay in Washington State. These copepods had full guts, the phytoplankton concentrations were higher than the laboratory determined I_{max}, their egg production rates were high, and their development times were near the fastest expected for the field temperatures. Therefor, *Pseudocalanus* in Dabob Bay doesn't appear food-limited; Ohman argued that the population growth rate was controlled by predation. **Huntley & Lopez (1992)** extend McLaren's argument to copepods in general. They argue that copepod development time is readily predicted in lab & field and that there is little evidence for food limitation of copepods. **Miller (2004)** provides a recent overview of the ensuing controversy, arguing that copepods can be food-limited and their de

ARE DIATOMS TOXIC TO CALANOID COPEPODS?

Several studies have argued that a diet of diatoms has sublethal toxic effects on calanoid populations. **Ban et al. (1997)** is a paper written by copepodologists from around the world, experienced in estimating egg production rates. They concluded that a diet of diatoms led to reproductive failure in copepods. **Miralto et al. (1999)** studied hatching success of eggs produced during a diatom bloom in the North Adriatic Sea. Only about 10% of *Calanus helgolandicus* eggs hatched during this bloom dominated by the diatoms *Skeletonema costatum* and *Pseudo-nitzschia delicatissima*. Toxic aldehydes were isolated from the diatoms which inhibited egg development in Calanus and in sea-urchin egg bioassays. **Irigoien et al. (2002)** didn't find a negative correlation between field hatching success and diatom abundance, suggesting that in field populations, copepods could supplement the deficient diatom diet with other prey, especially flagellates.

MODELING ZOOPLANKTON GRAZING

Most ecosystem simulation models include a strong functional relationship (usually a Monod relationship) between phytoplankton concentration and zooplankton ingestion rate (and growth rate). There are four major functional relationships used, first described first by **Holling 1959**: 1) rectilinear (or Holling Type 1), 2) Monod, Michaelis-Menten or Ivlev (Holling Type 2), 3) Sigmoid (Holling Type 3), and 4) a lag followed by sigmoid (Holling Type 4). **Frost (1972)** used a rectilinear model (*i. e.*, 2 straight lines-1 a horizontal asymptote) to model *Calanus pacificus* feeding. The 2-straight line model was called a Type 1 functional response by **Holling (1959)** (see Figure 1). The same data could be fit to a Holling Type 2 or Type 3 ingestion curve. **Holling 1959** used these curves to evaluate rodent predation on insects. Rodents exhibit a functional response showing an increased predation rate up to a saturated feeding level. When prey density exceeded this asymptote, insect outbreaks could result. The Michaelis-Menten equation is the most often used equation to describe grazing in ecosystem models:

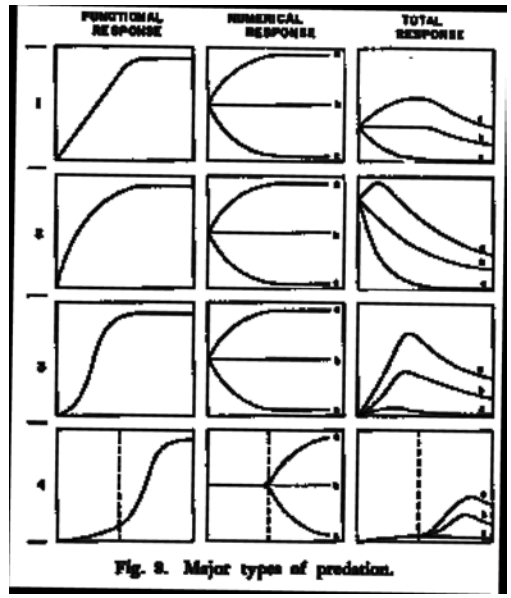

Figure 1. Type 1, 2, 3, and 4 Holling ingestion curves from **Holling (1959)**. The type 4 functional response curve (an asymmetric Type 3) is rarely discussed in the modern literature.

Michaelis-Menten Ingestion Equation:

$$I = I_m \left(\frac{P}{P_s + P}\right).$$

where, I = *Ingestion rate.*
P = *Phytoplankton concentration.*
P_s = *Half-saturation parameter.*
= *Phytoplankton concentration at which* $I = \frac{I_m}{2}$. **(2)**

The Ivlev equation requires only one parameter:

Ivlev equation:

$$I = I_m (1 - e^{-\delta P}). \quad \textbf{(3)}$$

A Holling Type 3 or Type 4 ingestion curve can be approximated by adding a feeding threshold, P_o, to a Michaelis-Menten or Ivlev equation:

Michaelis–Menten Ingestion Equation (with threshold):

$$I = I_m \left(\frac{P - P_o}{P_s + (P - P_o)} \right).$$

where, I = *Ingestion rate.*
I_m = *Maximum ingestion rate.*
P = *Phytoplankton concentration.*
P_o = *Feeding threshold*
P_s = *Half–saturation parameter.*
= *Phytoplankton conc. at which* $I = \frac{I_m}{2}$. **(4)**

Ivlev equation (with threshold):

$$I = I_m \left(1 - e^{-\delta (P - P_o)}\right). \quad \textbf{(5)}$$

Frost (1975) showed what appears to be a strong feeding threshold in the west coast equivalent of the Atlantic's *Calanus finmarchicus*, *Calanus pacificus*. **Lam & Frost (1976)** applied optimal foraging theory to copepod grazing, showing that a Holling Type-3 functional response curve was the resultant 'optimal' behavior. Optimal foraging theory can be used to predict what set of behaviors will lead to the maximum amount of food intake per unit time, given the biomechanical and physiological constraints of foraging for the animal of interest. **Lehman (1976)** published an optimal foraging model for grazers in the same volume of Limnology and Oceanography as **Lam & Frost (1976)**. Using a different approach, Lehman came to a similar conclusion: a Type 3 functional response curve was the expected optimal feeding behavior. A Type 3 functional response curve can produce an ingestion *vs*. phytoplankton concentration curve that closely resembles a Holling Type 2 functional response curve with a threshold.

Usually, the copepod ingestion rate of large cells is higher than that on small. This can be explained both by the leaky-sieve hypothesis and the low Re chemical plume hypotheses. Small cells are not eaten as efficiently as large because these either pass through the setules of the 2nd maxillae (unlikely) or they are not detected as effectively.

Although the ingestion rate of zooplankton increases with individual size, this increase is usually not linear:

$$I_{max} = \beta \, Z_{mass}^{\alpha},$$

where, I_{max} = *Maximum ingestion rate.* **(6)**
Z_{mass} = *Individual grazer weight.*

Since α is less than 1. 0 (usually 0. 7 or 0. 75 is assumed), the weight specific ingestion rate decreases with increasing individual grazer weight. Thus, a gram of copepodite Stage III's will ingest more phytoplankton in a day than a gram of copepodite stage VI's.

As phytoplankton becomes limiting, development times increase. **McLaren (1978)** reviewed the literature on copepod field development rates and, since the rates were close to optimal, concluded that copepod populations in nature are not food limited. That would certainly simplify ecosystem simulation modeling, but at the cost of abandoning much of our accepted knowledge about copepod grazing and growth.

POLICY IMPLICATIONS OF LOW RE FEEDING: OMNIVORY BY *ACARTIA*

In October 1995, the Barnstable County Science Advisory Panel issued a critique of the MWRA's monitoring of MA Bay. They argued that the key trophic links that lead from nutrient input to right whales had been given short shrift in the first four years of MWRA plankton modeling. In response the MWRA proposed a new hypothesis to assess whether the outfall would have an effect on large calanoid copepods, the preferred food of the endangered northern right whale.

As documented by **Turner (1984)**, there is a clear transition between the inshore and offshore calanoid copepod populations. The dominant zooplankton in biomass and abundance in the Boston Harbor and Inner Broad Sound area are the calanoid copepods *Acartia clausi* and *Acartia hudsonica*. The offshore population is numerically dominated by the small copepod *Oithona similis*. The key offshore copepods of regulatory concern are the calanoid copepods *Calanus finmarchicus* and *Pseudocalanus*. **Paffenhöfer & Stearns (1988)**, based on high-speed movies of feeding, proposed that *Acartia* was restricted to the nearshore zone because it requires high concentrations of phytoplankton to survive. **Paffenhöfer & Stearns (1988)** briefly review other hypotheses, such as vulnerability to predation offshore, but discount them. The MWRA and its consultants, following this food limitation hypothesis, argued that the transition from *Acartia* to *Oithona* could be used as an indicator of changed conditions in MA Bay. If *Acartia* were to dominate sites in outer MA Bay after the outfall went out, then the MWRA would consider implementing changes in the outfall.

The question of why *Acartia* is found only in the nearshore is more complex than the simple Paffenhöfer-Stearns hypothesis proposes. First, this pattern is very general. *Acartia* dominates in nearshore zones throughout North America. The same *Acartia* → *Calanus* transition occurs on the West Coast (Barnett & Jahn 1987) & the Gulf of Mexico (**Gifford & Dagg 1988**). *Acartia* is the numerical & biomass dominant of the zooplankton in Narragansett Bay & in **Kremer & Nixon's (1978)** Narragansett Bay Ecosystem model. The inadequacies of *Acartia* feeding on phytoplankton have been known for some time. Ecosystem modelers & copepodologists have struggled trying to figure out what *Acartia* was eating, especially in the winter. **Heinle *et al.* (1977)** argued that *Acartia* was feeding on detritus. **Roman (1985)** found that Acartia couldn't survive entirely on detritus, but detritus could supplement a diatom diet. **Kremer & Nixon (1978)** modeled *Acartia* as a cannibal, which could prey on any zooplankton smaller than itself, especially the naupliar & copepodite juvenile stages of its own population. The key paper

showing that *Acartia* was more than a herbivore was **Stoecker & Egloff (1987)** who argued that *Acartia* was feeding primarily on tintinnids & large ciliates. **Gifford & Dagg (1988)** estimated the grazing rates of *A. tonsa* on phytoplankton & microzooplankton. They found that *A. tonsa* feeds selectively on microzooplankton, but does ingest phytoplankton. During the winter, when microzooplankton prey are scarce, phytoplankton dominate the food intake of *A. tonsa*.

Just as **Paffenhöfer & Stearns (1988)** used high-speed cinematography to document the inadequacies of *Acartia* in detecting & clearing phytoplankton cells, **Jonsson & Tiselius (1990)** document the acute raptorial abilities of *Acartia* in finding & ingesting planktonic ciliates. They conclude:

> *"The potential for A. tonsa to switch between raptorial & suspension-feeding behavior may be a key in explaining their ubiquity in coastal waters. . . Acartia tonsa is not a representative true suspension feeding copepod since it engages in suspension feeding only a small fraction of the time, whereas a typical suspension feeder like Paracalanus sp. allocates >80% of the time to this feeding mode. "*

Jonsson & Tiselius (1990) argue that *Acartia* is a predator most of the time. While other copepods are beating their feeding appendages in order to detect phytoplankton by chemoreception, *Acartia* sits & waits for prey which it detects by mechanoreception. Using mechanoreceptors (*i. e.*, vibration detectors) may be incompatible with active suspension feeding with feeding currents. Another factor, cursorily dismissed by **Paffenhöfer & Stearns (1988)** is differential susceptibility to predation. *Acartia* is a small copepod that may be especially vulnerable to invertebrate predators. Table 1, modified from **Kremer & Nixon (1978)** shows the small relative size of *Acartia clausi* relative to *Pseudocalanus* & *Calanus*.

Table 1. Comparison of some copepod sizes & development times.

	Acartia. clausi	*Pseudocalanus*	*Calanus*
Naupliar mass (µg C)	0. 01	0. 07	8
CV mass (µg C)	2. 56	8	100
Developmental time (12°C) days	30	26	26
Developmental time (10°C)	34	36	

Now, that poses an interesting question, "How would the invertebrate predators, which use mechanoreception, detect *Acartia*?" The seasonal transition from wintertime herbivory to summertime raptorial feeding might be a response to invertebrate predators as well as the relative food quality of prey. When feeding in a raptorial mode (*i. e.*, no feeding currents), *Acartia* would be nearly undetectable by other invertebrate predators relying on mechanoreception. This hypothesis is consistent with another bit of information about the Boston Harbor Massachusetts

Bays copepods. The numerically dominant copepod offshore in MA Bay is another predator on ciliates, *Oithona similis*. **Turner (1984)** argues in his discussion section that *Oithona* may not feed on phytoplankton much at all, but instead it is a ciliate predator. Now, **Yen (1982)** documented that the invertebrate predator *Euchaeta elongata* was highly successful attacking small *Pseudocalanus*, but was ineffective in attacking large *Calanus pacificus* or the small *Oithona similis*. *Euchaeta elongata* uses mechanoreception to find prey. It is possible that this predatory copepod detects the feeding currents generated by *Pseudocalanus*, but not by *Oithona* or *Acartia*. It is unsuccessful feeding on the large *C. pacificus*, because large copepods are too large to handle. Thus, while **Gifford & Dagg (1988)** document that *Acartia* relies more-and-more on raptorial feeding from December → August, perhaps some of this transition may be due to the seasonal increase in invertebrate predators in coastal ecosystems. Suspension feeding *Acartia* would be far more likely to be detected & ingested by invertebrate predators.

Two final issues may be important in explaining the inshore → offshore transition from *Acartia* to *Pseudocalanus*. First *Acartia* produces a resting or diapause egg stage found in sediments. These resting eggs apparently require shallow sediments (<60 m). Finally, **Heinle et al. 's (1977)** idea that *Acartia* can utilize detritus, far more abundant in the nearshore, cannot be ruled out as a factor in the inshore → offshore transition.

Outlines of Papers

ASSIGNED

Koehl, M. A. R. & J. R. Strickler. 1981. Copepod feeding currents: food capture at low Reynold's number. Limnol. Oceanogr. *26*: 1062-1073. *[The paper that changed the way people analyzed copepod grazing.]* [3, 4, 5]

1.1 Abstract
1.2 High speed cinematography of dye streams of *Eucalanus plieatus*.
1.3 Re of only 10^{-2} to 10^{-1}
1.4 Water flow is laminar.
1.5 Old view of copepod feeding.
- 1.5.1 Cannon, Russell-Hunter, Barnes
- 1.5.2 Water flows through the second maxillae
- 1.5.3 Figure 1, part B: old view

1.6 New view
2nd maxillae not held constant
1.7 Methods
- 1.7.1 feeding on *Gymnodinium nelsoni* (50-53 µm)
- 1.7.2 *Thalassiosira weissflogii* (10-14 µm)
- 1.7.3 watermarked with india ink
- 1.7.4 Table 1
  Re 10^{-2} to $2 * 10^{-1}$

1.8 Results & discussion
- 1.8.1 flapping of other feeding appendages produces pulsing stream of water past the copepod
- 1.8.2 can sweep out 300 mls of water in 24 h.
- 1.8.3 organisms cannot filter that much water with the observed velocities of water
- 1.8.4 vortex-creating "fling" of insect wings
- 1.8.5 the water is squeezed out between the setae of the 2nd maxillae
- 1.8.6 Low Reynolds number

Re = ρ * v L/μ, ratio of inertial to viscous forces, μ is the dynamic viscosity
1.8.7 even the maximum Re are very low
1.8.8 water flow is laminar
1.8.8.1 water is not mixed
1.8.8.2 flapping does not stir the water
1.8.8.3 small appendages work more like paddles than rakes.
1.8.8.4 water resists flowing between closely spaced setules.
"A copepod appendage cannot strain an alga out of water as we might catch a ball using a scoop net; rather copepods must maneuver particles by moving the water surrounding the particles. A copepod appendage can, however, grab a particle with the tips of the setae (the "chopsticks" method)"
1.8.8.5 getting captured algae "unstuck" is not small feat.
1.8.9 copepods feed intermittently
1.8.10 selective feeding using mechanical or chemical cues.

Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. [*Read Chapter 7 pp. 129-146 on zooplankton grazing. Skim Chapter 6, an overview of zooplankton]*

7 Production Ecology of Marine zooplankton
7.1 Feeding mechanics
7.1.1 Figure 7. 1 Retention efficiency of two salp species
7.1.2 Appendicularian filtering: tangential flow filter
7.1.3 Koehl & Strckler (1981) *Eucalanus* movies
7.1.3.1Box 7. 2
7.1.3.2 Particle capture of *Euchaeta*

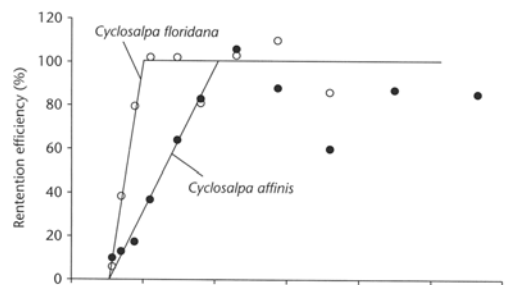

Fig. 7.1 Retention efficiency of the mucous filtering screens of two salp species as a function of particle size.

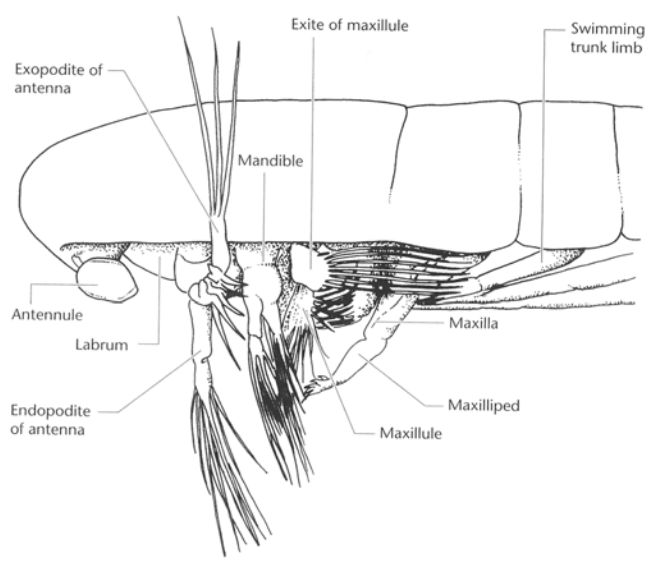

Fig. 7.2.1 Lateral view of the feeding limbs of *Calanus*. (After Cannon 1928.)

Figure 2. Miller (2004) Box Fig. 7. 2. 1 Feeding limbs of *Calanus*

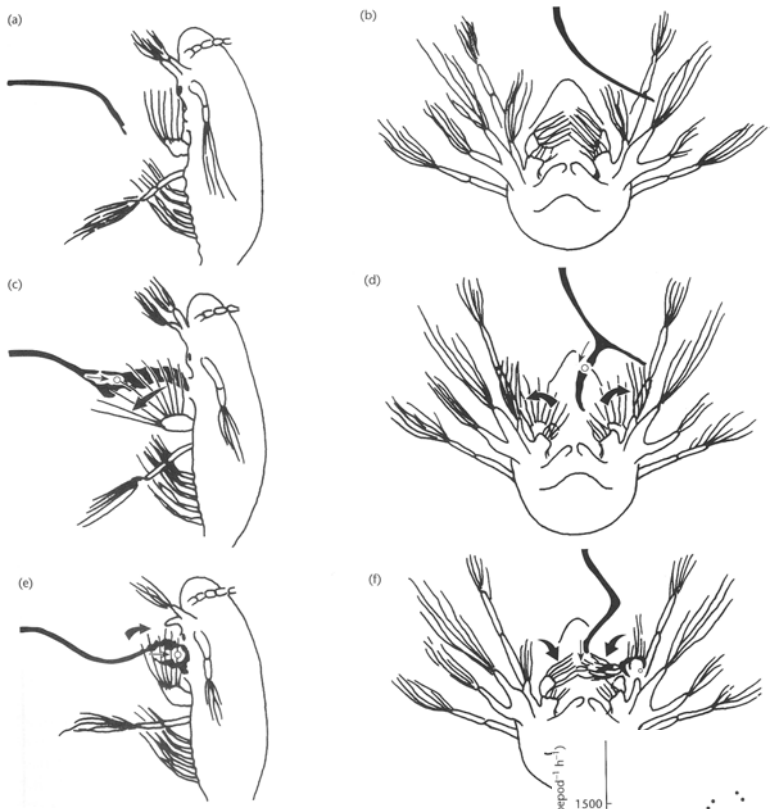

Figure 3. Miller (2004) Box Fig. 7. 2. 1 Fe
Calanus

pileatus Figure 7. 3

7.2 Feeding rates & factors affecting them

7.2.1 Frost (1972), see Fig. 7. 4

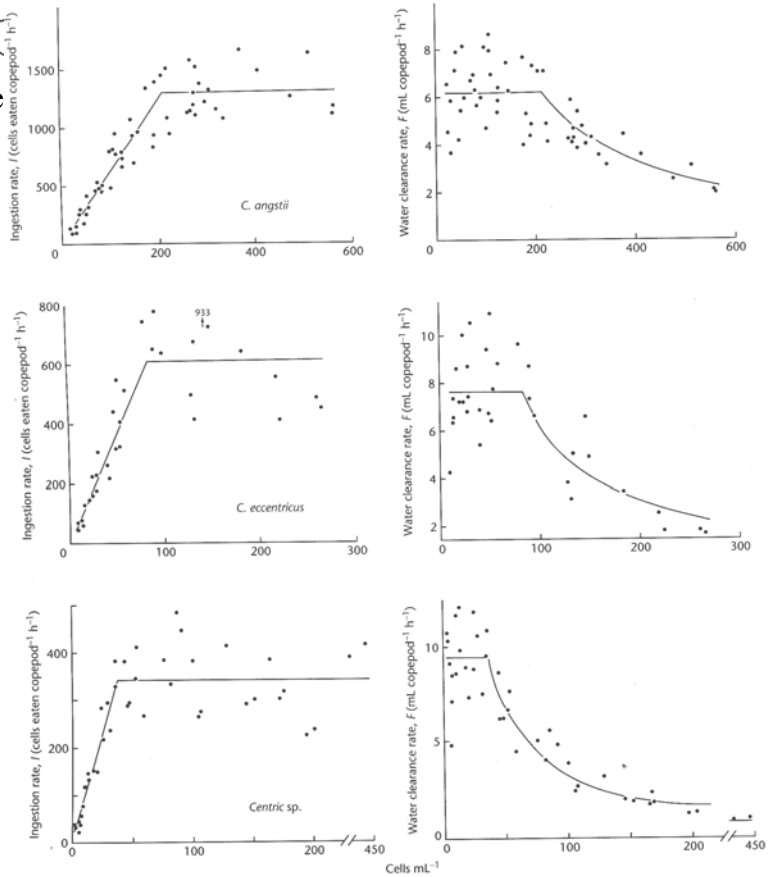

Fig. 7.4 Effect of cell concentration on ingestion rate (I, cells eaten copepod^{-1}h^{-1}, left) and water clearance rate (F, mL copepod^{-1}h^{-1}, right) in *Calanus pacificus* females feeding on three small-, medium-, and large-sized diatoms. (After Frost 1972.)

Figure 4. Miller (2004) Figure 7. 4 from Frost (1972)

SUPPLEMENTAL

Båmstedt, U., D. J. Gifford, X. Irigoien, A. Atkinson, and M. Roman. 2000. Feeding. Pp. 297-399 *in* R. Harris, P. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley, eds., ICES Zooplankton Methodology Manual. Academic Press, San Diego. 684 pp.

8 Feeding
- 8.1 Introduction
- 8.2 Feeding mechanisms of zooplankton
  - 8.2.1 Liquid feeders, microphages, macrophages
  - 8.2.2 Macrophage feeding modes
    - 8.2.2.1 Mobility
      - 8.2.2.1.1 ambush
      - 8.2.2.1.2 cruising
    - 8.2.2.2 prey capture
      - 8.2.2.2.1 entangling
      - 8.2.2.2.2 raptorial
    - 8.2.2.3 prey detection
      - 8.2.2.3.1 visual
      - 8.2.2.3.2 tactile
      - 8.2.2.3.3 chemosensory
- 8.3 Expression of zooplankton feeding rates and common conversion factors
  - 8.3.1 Clearance rate (F)
  - 8.3.2 Ingestion rate (I)
  - 8.3.3 Daily ration
  - 8.3.4 Conversion between units of mass and energy
- 8.4 Microzooplankton
  - 8.4.1 Methodological approaches

Table 8. 1 Methods to measure microzooplankton grazing

  - 8.4.2 Indirect methods to measure assemblage grazing
    - 8.4.2.1 Correlation of natural consumer-prey cycles
    - 8.4.2.2 Extrapolation of lab rates to the field
    - 8.4.2.3 The pigment budget (Welschmeyer & Lorenzen 1989)
    - 8.4.2.4 Acid lysozome assay
  - 8.4.3 Direct methods to measure per capita grazing rates
    - 8.4.3.1 Food tracers: inert particles
    - 8.4.3.2 Food tracers: prey cells
    - 8.4.3.3 Food tracers: radioisotopes
    - 8.4.3.4 Food vacuole contents
    - 8.4.3.5 Prey removal
  - 8.4.4 Direct methods to measure assemblage grazing rates
    - 8.4.4.1 Sea water dilution method
      - 8.4.4.1.1 Working procedures for the sea water dilution method
        - 8.4.4.1.1.1 Water collection
        - 8.4.4.1.1.2 Filtration
        - 8.4.4.1.1.3 Number of treatments and replicates
        - 8.4.4.1.1.4 Filling the incubation bottles
        - 8.4.4.1.1.5 The question of nutrient additions
        - 8.4.4.1.1.6 The problem of initial treatments
        - 8.4.4.1.1.7 Incubation conditions
        - 8.4.4.1.1.8 Data analysis
      - 8.4.4.1.2 Size fractionation methods
- 8.5 Meso- and macrozooplankton
  - 8.5.1 Empirical relationships

Table 8. 2 Overview of commone methods

  - 8.5.2 Field investigation on gut fluorescence
  - 8.5.3 Working procedure for the gut fluorescence method
  - 8.5.4 Gut contents of field sampled consumers

Banse, K. 1992. Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. Pp. 409-440 *in* P. G. Falkowski and A. D. Woodhead, eds., Primary Productivity and Biogeochemical Cycles in the Sea. Plenum Press, New York. *[An excellent review of the global importance of zooplankton grazing and nutrient regeneration. Banse divides the ocean into 3 domains. The 1st domain includes the so-called oligotrophic gyres, the second the High Nutrient Low Chlorophyll a zones (e. g., Station P), and the 3rd domain includes the classic N. Atlantic bloom region. Banse points out the central importance of grazing and nutrient regeneration in all three zones and illustrates his arguments with estimates of the relative importance of grazing to the other terms in the advection-diffusion-growth model of phytoplankton]* [**3**, **4**]

I. INTRODUCTION.
A. Parochial questions based on global Chl *a* maps:
(1) Where, (2) when, and (3) why does phytoplankton occur in the open sea, and (4) how much is found?
B. High Chl *a* associated with vertical transport of NO_3^-
C. 4th question: being handled through bio. oceanographic models.

II. THE ROLE OF GRAZING IN THE CONCENTRATION BALANCE.

A. The large-scale Geographic distribution of temporal change

1. Fig. 1 depicts Banse's view of the division of the Pacific and Atlantic oceans.
2. Domain 1 & 2: relatively little seasonal changes.
   a. Domain 1: permanent depletion of macronutrients
   b. Domain 2: macronutrients present.
3. Domain 1:
   -oligotrophic subtropical gyres.
4. Domain 3: Adjoins domain 1 on the poleward side.
   a. North Atlantic, Parts of S. Atlantic, South of Station P
   b. Weather Station M, Norwegian Sea.
5. Domain 2:
   a. No spring bloom, nor marked phytoplankton seasonality.
   b. Drake Passage.
   c. Appreciable winter phytoplankton are a requirement leading to a lack of spring bloom.
   d. Smetacek *et al*. (1990) provide further information on the lack of spring blooms in the southern ocean.
6. Domain 3: significant change.

Fig. 1. Estimated zones of Domains 1-3 in the world's ocean

B. The average daily rate of seasonal change of phytoplankton

1. CZCS
2. N. Pacific 1. 7% d^{-1}
3. North Indian: 11% d^{-1}

C. The effect of horizontal advection or diffusion on phytoplankton concentrations: model to be used includes only vertical transport.

D. The Temporal balance of phytoplankton and zooplankton in domains 1 and 2.

Fig. 2. Conceptual model to show the role of grazing [using the advection diffusion equation with estimates of the magnitudes of the terms.]

"The principal result of the modeling exercise (Fig. 2B) is that the measured algal division rates and the relatively small physical terms can be reconciled only by very large death rates (g) of phytoplankton, when the seasonal change (as d^{-1}) is slow, as observed. " p. 414.

1. The temperature dependence of g has several causes:
   a. The realized growth rates of the phytoplankton in the allegedly oligotrophic central gyres is remarkably high in absolute terms and relative to the "Eppley value"
   b. In cold nutrient-rich water during summer, it is again the lid on algal growth rate that proximally drives the system.
   c. because g equals the volume swept clear (F) by grazers. . . optical properties affected.
      (1) The temporal balance of phytoplankton and zooplankton in domain 3
2. Evans and Parslow's (1985) and Frost's models reviewed.
3. Fasham *et al*. (1983) Celtic Sea model.
4. Spring bloom declines
   a. Grazing
   b. Settling of live cells
      (1) Alldredge and Gotschalk (1989)
      (2) Jackson (1990)
      (3) Kjorboe *et al*. (199)
      (4) Passow (1991)
5. Fall blooms:
   a. *"Fall blooms in domain 3 depend on nutrient injection upon the diminishing of thermal stratification. "* p. 417
   b. Grazing (or lack of it) plays a role. Higher light required for a fall bloom to compensate for higher grazing and respiration costs (Riley 1967)

E. On Meso-scale spatial relations between phytoplankton and zooplankton
-Within a region, there can be negative correlations between Chl *a* and zooplankton: Hardy's refuted animal exclusion theory

III. Mechanisms of phytoplankton control by grazing.
- A. Phytoplankton cell numbers as affected by grazing.
- B. Division rates of grazers and phytoplankton.

  ". . . note that the small grazers that eat the generally small phytoplankton in Domains 1 and 2, can, at optimal (satiating) food levels, grow as fast or (greatly) faster than algae of the same size." p. 420
- C. Phytoplankton cell sizes as affected by grazing.

  "Recently, numerous heterotrophic dinoflagellates were shown to catch and digest extracellularly by a pseudopodial "pallum" so that cells or colonies like the diatom Chaetoceros, much larger than the dinoflagellate, can be used (Jacobson and Anderson, 1986, another mechanism in Hansen 1991)." p. 420-421

IV. GRAZING, DISSOLVED ORGANIC MATTER, AND THE MICROBIAL LOOP.

The main source of DOM may be sloppy feeding.

Fig. 3. Flow of material in the microbial loop.

V. HISTORICAL INTERACTIONS IN MARINE PHYTOPLANKTON AND ZOOPLANKTON RESEARCH
- A. Phytoplankton dynamics.
  1. Hensen (1887)
  2. Lohmann (1903) discovered nanoplankton
- B. The Nanozooplankton
- C. The Inexplicable delay of synthesis

Fig. 4. Riley's Georges Bank model.

Why wasn't Riley's 1946 paper accepted as the new paradigm showing the couple of phytoplankton and zooplankton grazing?

VI. CONCLUSION.
- A. Obstacles: (1) attitudes, and (2) system-inherent problems, and (3) the lure of new methods currently being directed.

  "Addressing the first obstacle, I wonder whether the teachers of biological oceanography, including myself, during the last four or five decades (since the theory was developed by Riley, Cushing and Steele) have to accept considerable blame for the neglect of grazing effects on temporal and spatial distributions of phytoplankton, and more generally, of feedback between zooplankton and phytoplankton. If so, change will be slow in coming, because even if all teachers changed their ways henceforth, the manpower pool in biological/chemical oceanography turns over slowly. Without new attitudes, however, new methods will lose much of their potential impact. Improvements of outlook would result from teaching biological oceanography in more process-oriented ways, including enhanced use of differential equations; from the publication of the near-perfect textbook (i. e., several of us should try it, in spite of the small market that will discourage publishers); and from embellishing the old art of teaching with the aid of new tools, e. g., software (distributed like books) for models of the subjects treated herein, which allow experimentation in classrooms and lab sections for the mutual education of teachers and students."

Frost, B. W. 1980. Grazing. Pp. 465-491 *in* I. Morris, ed., The Physiological ecology of phytoplankton. Blackwell's, Edinburgh. [3, 4, 6] (a) Grazing

- B. Introduction:

  Harvey (1935) & Riley (1946) modeled the importance of grazing on phytoplankton standing stock & production.
- C. Components of grazing

$$dP_i/dt = {}_{\Pi}(k_i - g_i) \qquad (13.\ 1)$$

[Note that Frost's k_i is μ, the specific growth rate]

$$P_{it} = P_{io}\, e^{(ki - gi)*t} \qquad (13.\ 2)$$

$$P_t = \Sigma\, P_{ii} \qquad (13.\ 3)$$

Fig. 13. 1. 3 types of ingestion curves. ${}_{\Pi}$ vs Filtration rate (volume filtered per unit animal per time)

1. Michaelis-Menten
2. Ivlev
3. Hollings' Type 3 ingestion curve (**Holling 1959**)

Fig. 13. 2 Particle retention curve F_i vs. D_i (concave down curve)

Table 13. 1. Effects of nonselective grazing on phytoplankton size composition. The relative abundance can be completely changed by selective grazing.

4. Zooplankton body size is important
5. Remineralization is directly coupled to zooplankton grazing

D. Estimation of grazing rates
1. monitoring change in phytoplankton concentrations
2. Laboratory measurements
   a. P vs Ingestion curves
   b. egg production rates
   c. enzyme activity (**Mayzaud & Conover (1984)**, **Head & Conover [1983]**, **Head *et al.* (1984)**, Faulbel & Meyer-Reill)
   d. gut-fullness measures
3. particle fluxes: pheophorbide fluxes

E. GRAZING & THE DYNAMICS OF PHYTOPLANKTON
1. grazing in seasonally variable environments

Fig. 13. 3.

   a. Why do we have a spring bloom?
   b. SUPER story
2. grazing in seasonally stable environments
   a. Low, stable phytoplankton standing stocks
   b. Nutrient regeneration is crucial: CARNEX model

Table 13. 3A. Doubling times should be 10. 35 days & 4. 29 days.

3. spatial & diel variation in grazing: diel vertical migration
4. changes in species composition: Steele & Frost model

Price, H. J. 1988. Feeding mechanisms in marine & freshwater zooplankton. Bull. Mar. Sci. *43*: 327-343. [6]

1 Abstract
traditional view replaced
2 Introduction
2.1 earlier review by Conover
2.2 Optimal foraging theory.
3 Technical advances.
3.1 SEM
3.2 High speed cinematography
4 Components of predation model.
Holling 1959 components of predation.
$_{\Pi}=P_E+P_P*P_C*_{\Pi}$
5 Encounter
5.1 Remote detection
5.1.1 algal cells detected several hundred µm away.
5.1.2 Csanady (1986) calculated that the energy from large-scale eddies will not be propagated to scales smaller than 1 mm, so that shear associated with the smallest eddies should not distort diffusion around most organic particles.
5.2 Chemoreception vs. Mechanoreception
5.2.1 extracellular release is a normal process (Mague *et al.*, 1980, Hamner & Brockman 1983). excretion may increase as the population enters stationary phase (Poulet & Marin-Jezequel 1983).
5.2.2 mechanoreception
5.3 Specificity of signals.
6 Pursuit
7 Capture
7.1 Low amplitude flapping of the second maxillae drives the cells between the setae & they are funneled across the appendage to the mouth without adhering to the setules.
7.2 sieving invoked for ciliates.

8 Ingestion
9 Conclusions

Purcell, A. M. 1977. Life at low Reynolds number. Am. J. Physics. *45*: 3-11. [5]
I. Introduction
A. no liquid with a viscosity lower than water [10^{-2} cm^2 s^{-1}]
B. Low Re regime
C. How do microorganisms swim: Berg
Fig. 2 η^2/ρ is a force
for water $\eta^2/\rho = 10^{-4}$
This force will tow anything, large or small at Re≈1
Fig. 3. Re for organisms
1. for a man swimming is Re≈10^4
2. For a goldfish, Re≈10^2
3. For a bacterium ≈10^{-4}
Fig. 4. 1 µm bacterium swimming
v=30 µm s^{-1}
v=10^{-2} cm^2 s^{-1}
Re=3 x 10^{-5}
D. How far will a bacterium coast: 0. 1 angstrom
E. Purcell's story of low Re life:
"It helps to imagine under what conditions a man would be swimming at, say, the same Re as his own sperm. Well, you put him in a swimming pool that is full of molasses & then you forbid him to move any part of his body faster than 1 cm/min. Now imagine yourself in that condition: you're under the swimming pool in molasses, & now you can only move like the hands on a clock. " (P. 4)
F. Reciprocal motion doesn't work.
G. if you take the Navier-Stokes equation & throw away the inertial terms, all you have left
H. scallops can't swim in a low Re regime.
Fig. 10. Real bacteria (schematically drawn)
Fig. 11. Berg's tumble & run.
II. Energy required to swim: p. 9: *"Bacteria are driving a Datsun in Saudi Arabia. "*
III. Diffusion: the bugs problem is not energy, it is its environment
A. Food supply just sitting still is 4πaND molecules/sec, where a is the cell's radius, & N is the concentration of nutrient molecule. To increase its food supply by 10% it would have to move 20 times as fast as it can swim. The bug can't find more molecules in a relatively homogeneous environment, but it can find better patches.
B. How far does a bug have to move? Well it has to outrun diffusion. D/v 10-5 cm^2 s^{-1}/v, where v≈3 x 10-3 cm s^{-1} ≈33 µm
Fig. 20. How far would a 30 µm s^{-1} swimmer have to swim to outrun diffusion: 30 µm

Welschmeyer, N. A. and C. J. Lorenzen. 1985. Chlorophyll budgets: zooplankton grazing and phytoplankton growth in a temperate fjord and the Central Pacific gyres. Limnol. Oceanogr. *30*: 1-21. *[Following Shuman's discovery that Chl a is stoichiometrically converted to pheophorbide a in copepod guts, W & S balance the water-column grazing budget, calculating the relative importance of macro- & microzooplankton grazing.]*[4, 26]
IV. Abstract
A. Dabob Bay and the oligotrophic ocean compared
B. Dabob Bay
1. spec. growth = 0. 05-0. 9 d^{-1},
2. 67% of grazing due to macrozooplankton
C. Gyres
1. µ = 0. 2 d^{-1},
2. 95% of grazing due to microzooplankton
V. Introduction
A. define interactions among processes affecting chl and pheopigments
B. id and quantify dominant processes
C. calculate growth and zooplankton grazing

VI. The formation and fate of chl
- A. stoichiometric pigment conversion
- B. standard fluorometric technique does not distinguish h pheophytin a from pheophorbide a
- C. vertical distributions dissimilar
- D. fecal pellets sink at 100 m/d
- E. pheopigments degraded by light

VII. Methods
- A. Dabob
- B. gyre:
  1. 100-120 m chl max.
  2. 20 mg Chl a / m^{-2}
- C. sed traps
- D. effects of dankness on pigment content
  1. dark degradation of sed. trap material
  2. photodegradation of pheophorbide: strange--why weren't the bottles poisoned to eliminate production terms

VIII. **Results**:
- A. cellular pigment content
- B. photodegradation: $P_t=P_o \exp(-k_I I)$, where I is Einst/m² PAR
  1. important loss term

Table 2: daily ^{14}C production in Dabob **0. 024 to 1. 6 g C, in the gyres it is 0. 06 to 0. 11 g C.**
- C. A complete pigment budget:

Figure 8
- D. chl flux only 10% of pheophorbide flux
- E. macrozooplankton dominate grazing in Dabob (47-95% with mean=67%)
- F. micro dom. grazing in gyres (5% by macrozooplankton)
- G. mixing is not important. 200x less than microzoop grazing.
- H. Redalje technique used to estimate C:chl ratios
  1. Dabob: 13-85, avg=42.
  2. Gyres. 11-24 (wet weight), mean = 17, high C:chl ratios expected. Sharp expected 114.
- I. Lorenzen has measured Carbon fluxes of >100mgC$m^{-2}d^{-1}$, these rates are greater than ^{14}C production. Therefore, the estimates of primary production may be way too low. The real rates may be 0. 5 g C/da

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Grazing at low Re, the leaky sieve hypothesis, & chemoreception

Alcarez, M, G. -A. Paffenhöfer, & J. R. Strickler. 1980. Catching the algae: a first account of visual observations on filter-feeding calanoids. Pp. 241-248 *in* W. C. Kerfoot, *ed*., Evolution & ecology of zooplankton communities. University Press of New England, Hanover, New Hampshire, U. S. A. *[This is one of the first accounts of the effects of low Re on copepod feeding.]* [?]

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Cowles, R. J., R. J. Olsen, & S. W. Chisholm. 1988. Food selection by copepods: discrimination on the basis of food quality. Marine Biology *100*: 41-49. *[Actively growing phytoplankton cells are selected preferentially over senescent phytoplankton cells. This is in accord with the chemoreception theory of how calanoids find phytoplankton cells]*[**8**, **26**]

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Jackson, G. A. 1987b. Simulating chemosensory responses of marine microorganisms. Limnol. Oceanogr. *32*: 1253-1266. *[Bacterial-sized particles may not produce a sufficient chemical signal to be detected by a grazer; grazers may have to be contact feeders]*[**6**]

Jonsson, P. R. & P. Tiselius. 1990. Feeding behavior, prey detection & capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. Mar. Ecol. Prog. Ser. *60*: 35-44. *[High-speed movies indicate that Acartia tonsa is not a true suspension feeder, like most other calanoids. It is highly adapted at detecting & ingesting planktonic ciliates. It is also capable of feeding on phytoplankton, albeit poorly (****Paffenhöfer & Stearns 1988****), & this omnivorous feeding may account for the ubiquity of Acartia in nearshore ecosystems.]*[**12**]

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Koehl, M. A. R. & J. R. Strickler. 1981. Copepod feeding currents: food capture at low Reynold's number. Limnol. Oceanogr. *26:* 1062-1073. *[A classic, outlined above]* [**3**, **4**, **5**]

Lȩgier-Visser, M. J., J. G. Mitchell, A. Okubo, & J. A. Fuhrman. 1986. Mechanoreception in calanoid copepods. A mechanism for prey detection. Marine Biology *90*: 529-535. *[A simulation model in which copepods detect pressure disturbances which vary directly with particle size & inversely to the square of distance.]*

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Paffenhöfer, G. -A. & D. E. Stearns. 1988. Why is *Acartia tonsa* (Copepoda: Calanoida) restricted to nearshore environments? Mar. Ecol. Prog. Ser. *42*: 33-38. *[Movies show that A. tonsa is poor at detecting & clearing phytoplankton cells compared to Paracalanus. They propose that A. tonsa requires high phytoplankton cell densities to survive. However,* ***Jonnson & Tisselius (1990)*** *following* ***Stoecker & Egloff (1987)*** *argue that Acartia is probably an omnivore, deriving much of its energy from predation on tintinnids & large ciliates]*[**3**, **11**, **12**, **23**]

Paffenhöfer, G. A. & K. D. Lewis. 1990. Perceptive performance & feeding behavior of calanoid copepods. J. Plankton Res. *12*: *933-946. [High-speed movies of Eucalanus pileatus analyzed. The distance from which E. pileatus deteccts phytoplankton cells increases 2-fold as phytoplankton density declines, perhaps due to increased sensitivity to detect cells.]*[**4**]

Poulet, S. A. & P. Marsot. 1978. Chemosensory grazing by marine calanoid copepods (Arthropoda: Crustacea). Science *200:* 1403-1405.

Price, H. J. 1988. Feeding mechanisms in marine & freshwater zooplankton. Bull. Mar. Sci. *43*: 327-343. *[A brief review of the mechanisms by which zooplankton detect, pursue & ingest their prey.]*[**6**]

Price, H. J., G. -A. Paffenhöfer, & J. R. Strickler. 1983. Modes of cell capture in calanoid copepods. Limnol. Oceanogr. *28:* 116-123.

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Price, H. J. & G. -A. Paffenhöfer. 1986. Effects of concentration on the feeding of a marine copepod in algal monocultures & mixtures. J. Plankton Res. *8*: 119-128. *[High-speed cinematography is used to show that copepods have 2 capture modes & conserve energy at low food concentrations.]*

Price, H. J., G. -A. Paffenhöfer, C. M. Boyd, T. J. Cowles, P. L. Donaghay, W. M. Hamner, W. Lampert, L. B. Quetin, R. M. Ross, J. R. Strickler, & M. J. Youngbluth. 1988. Future studies of zooplankton behavior: questions & technological developments. Bull. Mar. Sci. *43*: 853-872. *[A plea for national zooplankton research centers.]*

Purcell, A. M. 1977. Life at low Reynolds number. Am. J. Physics. *45*: 3-11. *[A classic common-sense description of life at low Re & why it matters.]*[**5**]

Rothschild, B. J. & T. R. Osborne. 1988. Small-scale turbulence & plankton contact rates. J. Plankton Res. *10*: 465-474. *[Computer models of planktonic physics.]*

Strickler, J. R. 1982. Calanoid copepods, feeding currents, & the role of gravity. Science *218*: 158-160. *[An odd paper that argues that sinking helps copepods detect phytoplankton cells. I couldn't figure it out; maybe you can. . Nice pictures though.]*

Strickler, J. R. 1984. Sticky water: a selective force in copepod evolution. Pp. 187-239 *in* D. G. Meyers & J. R. Strickler, *eds*., Trophic interactions within aquatic ecosystems. Westview Press.

Strickler, J. R. 1985. [Comment on] Emlet & Strathman's Gravity, drag & feeding currents of small zooplankton. Science *228*: 1016-1017.

Vanderploeg, H. A. & G. -A. Paffenhöfer. 1985. Modes of algal capture by the freshwater copepod *Diaptomus sicilis* & their relation to food-size selection. Limnol. Oceanogr. *30*: 871-885. *[Two feeding modes, active for large cells, and passive for small cells (<4 µm) documented. The passive capture can not be analyzed as a leaky sieve. The 2nd maxillae in passive capture acts as a funnel, not a sieve.]*

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Azam, F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil, and F. Thingstad. 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. *10*: 257-263. [**4**]

Banse, K. 1992. Grazing, temporal changes of phytoplankton concentrations, & the microbial loop in the open sea. Pp. 409-440 *in* P. G. Falkowski & A. D. Woodhead, *eds*., Primary Productivity & Biogeochemical Cycles in the Sea. Plenum Press, New York. *[An excellent review of the global importance of zooplankton grazing & nutrient regeneration. Banse divides the ocean into 3 domains. The 1st domain includes the so-called oligotrophic gyres, the second the High Nutrient Low Chlorophyll a zones (e. g., Station P), & the 3rd domain includes the classic N. Atlantic bloom region. Banse points out the central importance of grazing & nutrient regeneration in all three zones & illustrates his arguments with estimates of the relative importance of grazing to the other terms in the advection-diffusion-growth model of phytoplankton]* [**3**, **4**]

Banse, K. 1994. Grazing & zooplankton production as key controls of phytoplankton production in the open ocean. Oceanography 7: 13-20. *[Review of pigment patterns in the subarctic Pacific, Equ. Pacific, & N. Pacific gyre, where pigment conc. doesn't change much & in the N. Sea where it does. Key research needs addressed.]*

Banse, K. 1995. Zooplankton: pivotal role in the control of ocean production. ICES J. mar. Sci. *52*: 265-277. *[Focus on oligotrophic waters. Primary production proportional to zooplankton N regeneration, due to sloppy feeding]*

Bengtssen, J. 1987. Smaller zooplankton are not superior in exploitative competition: a comment on Perrson. Amer. Natur. *129*: 928-931. *[One part of the Brooks & Dodson size-efficiency hypothesis predicts that large zooplankton are competitively superior. Many papers have refuted this part of the hypothesis.]*

Berggreen, U., B. Hansen, & T. Kiørboe. 1988. Food size spectra, ingestion & growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Marine Biology *99*: 341-352. *[Egg production rates can be used to infer past feeding history.]*[?]

Boyd, C. M. 1976. Selection of particle sizes by filter-feeding copepods: a plea for reason. Limnol. Oceanogr. *21*: 175-180. *[This paper, following **Nival & Nival 1973**, proposed the leaky-sieve hypothesis]* [**4**]

Carpenter, S. R., P. R. Leavitt, J. J. Elser, & M. M. Elser. 1988. Chlorophyll budgets: response to food web manipulation. Biogeochemistry *6*: 79-90. *[Uses the Shuman-Welschmeyer-Lorenzen pigment budget technique.]*

Checkley, D. M. 1980. The egg production of a marine planktonic copepod in relation to its food supply: laboratory studies. Limnol. Oceanogr. 25: 430-446. [*Paracalanus parvus*] {?}

Cloern, J. E. 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? Mar. Ecol. Prog. Ser. *9*: 191-202. *[Grazing by benthic suspension feeders]*

Conover, R. J., R. Duvasala, S. Roy, & R. Wang. 1986. Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton & some of the consequences. Limnol. Oceanogr. *31*: 878-886. *[Shuman & Welschmeyer found that chl a is converted completely to pheophorbide on passage through calanoids.* ***Welschmeyer & Lorenzen (1985)*** *used this principle to estimate calanoid grazing rates from sediment-trap data. This paper attacks the assumptions of* ***Welschmeyer & Lorenzen. (1985)****]*[?]

Cucci, T. L., S. E. Shumway, R. C. Newell., R. Selvin, R. R. L. Guillard, & C. M. Yentsch. 1985. Flow cytometry: a new method for characterization of differential ingestion, digestion & egestion by suspension feeders. Marine Ecology Progress Series 24: 201-204. *[The technique applied by* ***Cowles et al. 1988****)]*

Dagg, M. J. 1993. Grazing by the copepod community does not control phytoplankton production in the subarctic Pacific Ocean. Prog. Oceanogr. 32: 163-183. [?]

Dagg, M. J. & K. D. Wyman. 1983. Natural ingestion rates of the copepods *Neocalanus plumchrus* & *N. cristatus* calculated from gut contents. Marine Ecology Progress Series *13*: 37-46. *[These two copepods are the horse-fly sized calanoid copepods of the North Pacific. Their role in controlling the Spring phytoplankton bloom was the subject of Project SUPER.]*

Dagg, M. J. & W. E. Walser. 1987. Ingestion, gut passage, & egestion by the copepod Neocalanus plumchrus in the laboratory & in the subarctic Pacific Ocean. Limnol. Oceanogr. 32: 178-188.

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Downs, J. N. & C. J. Lorenzen. 1985. Carbon: pheopigment ratios of zooplankton fecal pellets as an index of herbivorous feeding. Limnol. Oceanogr. *30*: 1024-1036. [?]

Durbin, E. G., R. G. Campbell, S. L. Gilman, A. G. Durbin. 1995. Diel feeding-behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. Continental Shelf Research *15*: 539-570. *[Abstract: "In situ feeding was measured on late stage Calanus finmarchicus in the southern Gulf of Maine. . . a spring feeding ground for the planktivorous right whale. . . In situ ingestion rates of C. finmarchicus reflected these differences in food, and ranged from 30. 2% body C d^{-1} at a spring bloom station to 0. 6% body C d^{-1} after stratification. . . . C. finmarchicus became food limited in the southern Gulf of Maine after stratification. . . . Diel feeding rhythms and vertical migration were absent during the bloom, but developed as the bloom declined. During the post-bloom stratified conditions, diel feeding rhythms continued but vertical migration ceased. Most of the C. finmarchicus population remained near the surface, while a small population of nonmigratory individuals resided at depth and appeared to be feeding upon sedimented spring bloom diatoms. At the spring bloom station C. finmarchicus ingested only a small proportion of the phytoplankton standing stock in the >7 µm size fraction (2. 9% d^{-1}), reflecting the high biomass of phytoplankton and the stage composition of the C. finmarchicus population, dominated by early copepodite states with low biomass. In contrast, at the post-bloom stations in 1989, the dense surface aggregations of C. finmarchicus populations were dominated by late copepodite stages whose total biomass was comparable to that of the phytoplankton, and C. finmarchicus consumed a significantly larger fraction of the >7 µm phytoplankton standing crop (up to 62. 5% d^{-1}). "]*

Fenchel, T. 1980. Suspension feeding in ciliated protozoa: feeding rates and their ecological significance. Microbial Ecology *6*: 13-26. [?]

Fenchel, T. 1988. Marine plankton food chains. Ann. Rev. Ecol. Syst. *19*: 19-38. [**4**]

Frost, B. W. 1972. Effects of size & concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. *17*: 805-815. *[Frost demonstrated the ingestion rate of C. pacificus on single species of centric diatoms, showing a rectilinear ingestion response curve {similar to the (**Holling 1959**) Type 1 response} Ingestion rate expressed as phytoplankton carbon is the same for different sized diatoms, but at low concentrations, copepods have a higher carbon specific ingestion rate on large diatoms]*[**9**]

Frost, B. 1975. A threshold feeding behavior in *Calanus pacificus*. Limnol. Oceanogr. *20*: 263-266. *[Females fed Thalassiosira drastically reduced their clearance rate at low cell densities & relatively constant at high cell densities. This can be modeled with an Ivlev function with a feeding threshold - later **Lam & Frost (1976)** argued this functional response is consistent with a Holling type 3 ingestion curve* (**Holling 1959**)*]*[**10**]

Frost, B. W. 1977. Feeding behavior of *Calanus pacificus* in mixtures of food particles. Limnol. Oceanogr. *22*: 472-491. [**4**]

Frost, B. W. 1980. Grazing. Pp. 465-491 *in* I. Morris, *ed*., The Physiological ecology of phytoplankton. Blackwell's, Edinburgh. [*A key review describing the importance of grazers to the understanding of phytoplankton growth]*[**3**, **4**, **6**]

Frost, B. W., M. R. Landry, & R. P. Hassett. 1983. Feeding behavior of large calanoid copepods *Neocalanus cristatus* & *N. plumchrus* from the subarctic Pacific Ocean. Deep-Sea Research *30*: 1-13.

Gifford, D. J. 1988. Impact of grazing by Microzooplankton in the Northwest Arm of Halifax Harbour, Nova Scotia. Mar. Ecol. Prog. Ser. *47*: 249-258 [*Ciliates]*.

Gifford, D. J., L. M. Fessenden, P. R. Garrahan & E. Martin. 1995. Grazing by micro- & mesozooplankton in the high-latitude North Atlantic Ocean: spring versus summer dynamics. J. Geophys. Res. *100*: 6665-6675.

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Hansen B., P. K. Bjornsen, and P. J. Hansen. 1994. The size ratio between planktonic predators and their prey. Limnol. Oceanogr. 39: 395-403. *[Size ratio for ciliates is 8:1 and copepods 18:1]*

Harris, R. P., J. -F. Samain, J. Moal, V. Martin-Jezequel, & S. A. Poulet. 1986. Effects of algal diet on digestive enzyme activity in *Calanus helgolandicus*. Marine Biology *90*: 353-361.

Hassett, R. P. & M. R. Landry. 1983. Effects of food-level acclimation on digestive enzyme activities & feeding behavior of *Calanus pacificus*. Marine Biology *75*: 47-55. *[Poulet & Mayzaud felt that digestive enzyme activities could be used to estimate the feeding rates of zooplankton. Hassett found many flaws in this approach.]*

Hassett, R. P. & M. R. Landry. 1988. Short-term changes in feeding & digestion by the copepod *Calanus pacificus*. Marine Biology *99*: 63-74.

Hassett, R. P. & M. R. Landry. 1990a Effects of diet & starvation on digestive enzyme activity & feeding behavior of the marine copepod *Calanus pacificus*. J. Plankton Res. *12*: 991-1010. [**7**]

Hassett, R. P. & M. R. Landry. 1990b Seasonal changes in feeding rate, digestive enzyme activity, & assimilation efficiency of *Calanus pacificus*. Mar. Ecol. Prog. Ser. *62*: 203-210. [?]

Head, E. J. H. 1986. Estimation of Arctic copepod grazing rates *in vivo* & comparison with *in vitro* methods. Marine Biology *92*: 371-379. *[The feeding rates of C. hyperboreus & C. glaciales was estimated by measuring gut filling & fullness]*

Head, E. J. H. 1988. Copepod feeding behavior & the measurement of grazing rates *in vivo* & *in vitro*. Hydrobiologia *167/168*: 31-41. *[Head uses the gut-fluorescence method & documents pigment destruction in copepod guts.]*[**7**]

Head, E. J. H. & R. J. Conover. 1983. Induction of digestive enzymes in *Calanus hyperboreus*. Marine Biology Letters *4*: 219-231. [**7**]

Head, E. J. H., R. Wang, & R. J. Conover. 1984. Comparison of diurnal feeding rhythms in *Temora longicornis* & *Centropages hamatus* with digestive enzyme activity. J. Plankton Research *6*: 543-551. [**7**]

Head, E. J. H. & L. R. Harris. 1994. Feeding selectivity by copepods grazing on natural members of phytoplankton determined by HPLC analysis of pigments. Mar. Ecol. Prog. Ser. *110*: 75-83.

Head, E. J. H. & L. R. Harris. 1996. Chlorophyll destruction by Calanus spp. grazing on phytoplankton: kinetics, effects of ingestion rate & feeding history, & a mechanistic interpretation. Mar. Ecol. Prog. Ser. *135*: 223-235. *[Chl a destruction ranged from 20% to 100%. Degradation proposed to be due to both the copepods & phytoplankton cells enzymes & a function of ingestion rate & phytoplankton species composition]*

Heinle, D. R., R. P. Harris, J. F. Ustach, & D. A. Flemer. 1977. Detritus as food for estuarine copepods. Marine Biology *40*: 341-353. [**11**, **13**]

Houde, S. E. L. & M. R. Roman. 1987. Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa*. Mar. Ecol. Prog. Ser. *40*: 69-77.

Kerfoot, W. C. & K. L. Kirk. 1991. Degree of taste discrimination among suspension-feeding cladocerans & copepods: implications for detritivory & herbivory. Limnol. Oceanogr. : 1107-1123.

Lam, R. K. & B. W. Frost. 1976. Model of copepod filtering response to changes in size & concentrations of food. Limnol. Oceanogr. *21*: 490-500. *[The **Holling (1959)** Type 3 ingestion curve is one outcome of an optimal foraging model of copepod ingestion. **Lehman (1976)** produced a similar curve using a related model.]*[**10**, **29**]

Landry, M. R., R. P. Hassett, V. Fagerness, J. Downs, & C. J. Lorenzen. 1984. Effect of food acclimation on assimilation efficiency of *Calanus pacificus*. Limnol. Oceanogr. *29*: 361-364.

Lehman, J. T. 1976. The filter-feeder as an optimal forager, & the predicted shapes of feeding curves. Limnol. Oceanogr. *21*: 501-516. *[A Holling Type 3 functional response curve is the predicted optimal ingestion response.]*[**10**, **29**]

Liu, H., L. Campbell and M. R. Landry. 1995. Growth and mortality rates of *Prochlorococcus* and *Synechococcus* measured with a seletive inhibitor technique. Mar. Ecol. Prog. Ser. *116*: 277-287. [?]

Lopez, M. D. G., M. E. Huntley, & P. F. Sykes. 1988. Pigment destruction by *Calanus pacificus*: impact on the estimation of water column fluxes. J. Plankton Res. *10*: 715-734. *[Bodes ill for the Shuman-Welschmeyer-Lorenzen pigment budget approach to grazing.]*[?]

Mackas, D. & R. Bohrer. 1976. Fluorescence analysis of zooplankton gut contents & an investigation of diel feeding patterns. J. exp. Mar. Biol. Ecol. *25*: 77-99. *[Gut fluorescence]* [**7**]

Mallin, M. A. & H. W. Paerl. 1994. Planktonic trophic transfer in an estuary: seasonal, diel, & community structure effects. Ecology *75*: 2168-2184. *[Zooplankton grazing lowest in winter & highest in spring through late summer. Little diel variation. Grazing correlated with primary production. Annually, zooplankton grazed ≈38-45% of daily primary production.]*

Marin, V., M. E. Huntley, & B. Frost. 1986. Measuring feeding rates of pelagic herbivores: analysis of experimental design & methods. Marine Biology *93*: 49-58.

Mayzaud, P. & R. J. Conover. 1984. Distribution of digestive enzymes in zooplankton during the spring bloom in a Nova Scotia inlet. Can. J. Fish. Aquat. Sci. *41*: 245-252. *[The activity of digestive enzymes is used to infer the ingestion rates of copepods]*

Mayzaud, O., P. Mayzaud, C. dela Bigne, & P. Grohan. 1984. Diel changes in the particulate environment, feeding activity & digestive enzyme concentration in neritic zooplankton. J. exp. Mar. Biol. Ecol. *84*: 15-35.

Mayzaud, P. & S. Razouls. 1992. Degradation of gut pigment during feeding by a subantarctic copepod: importance of feeding history & digestive acclimation. Limnol. Oceanogr. *37*: 393-403. [7]

Mazumder, A., D. J. McQueen, W. D. Taylor B. R. S. Lean & M. D. Dickman. 1990. Micro- & mesozooplankton grazing on natural pico- & nanoplankton in contrasting plankton communities produced by planktivore manipulation & fertilization. Arch. Hydrobiol. *118*: 257-282.

McClatchie, S. & M. R. Lewis. 1986. Limitations of grazing rate equations: the case for time-series measurements. Marine Biology *92*: 135-140. *[Frost's grazing equations are found to lead to biased estimates of grazing rates.]*

Mobley, C. T. 1987. Time-series ingestion rate estimates on individual *Calanus pacificus* Brodsky: interactions with environmental & biological factors. J. exp. Mar. Biol. Ecol. *114*: 199-216.

Murtaugh, P. A. 1984. Variable gut residence time: problems in inferring feeding rate from stomach fullness of a Mysid crustacean. Can. J. Fish. Aquat. Sci. *41*: 1287-1293. [7]

Napp, J. M. & D. L. Long. 1989, A new isotope method for measuring diel grazing rates of marine zooplankton *in situ*. Limnol. Oceanogr. *34*: 618-629.

Ohman, M. D. 1985a. Resource-satiated population growth of the copepod *Pseudocalanus* sp. Arch. Hydrobiol. *21*: 15-32. *[Phytoplankton concentrations in Dabob Bay are higher than the I_{max} for ingestion in the lab, development times in the field are fast, & egg production high. ∴ Pseudocalanus population growth in Dabob Bay isn't food limited]* [7, 8]

Ohman, M. D. 1988b. Sources of variability in measurements of copepod lipids & gut fluorescence in the California Current zone. Mar. Ecol. Prog. Ser. *42*: 143-153. [7]

Paffenhöfer, G. -A. 1971. Grazing & ingestion rates of nauplii, copepodids & adults of the marine planktonic copepod *Calanus helgolandicus*. Marine Biology *11*: 286-298.

Paffenhöfer, G. -A. & K. B. Van Sant. 1985. The feeding response of a marine planktonic copepod to quantity & quality of particles. Mar. Ecol. Prog. Ser. *27*: 55-65.

Penry, D. L. and B. W. Frost. 1990. Re-evaluation of the gut fullness (gut fluorescence) method for inferring ingestion rates of suspension-feeding copepods. Limnol. Oceanogr. 35: 1207-1214. *[Ingestion can be estimated if egestion rate and fluorescence known. However, egestion rate is not a constant, making direct estimation of ingestion from fluorescence very difficult]* {7}

Penry, D. L. & B. W. Frost. 1991. Chlorophyll a degradation by *Calanus pacificus*: dependence on ingestion rate & digestive acclimation to food resources. Limnol. Oceanogr. *36*: 147-159.

Perrson, L. 1985. Asymmetrical competition: Are larger animals competitively superior? Amer. Natur. *126*: 261-266. *[see also Critique by Bengtsson]*

Peters, R. H. & J. A. Downing. 1984. Empirical analysis of zooplankton filtering & feeding rates. Limnol. Oceanogr. *29*: 763-784.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15: 523-575. *[Reviews the **Lam & Frost (1976)** & **Lehman (1976)** optimal foraging models for copepods.]*

Raven, J. A. and A. M. Waite. 2004. The evolution of silicification in diatoms: inescapable sinking and sinking as escape? New Phytologist *162*:1-45. *[A nice history of diatom evolution. Coevolution with parasites and grazers may have played a role in the adaptive radiation of silicified diatoms]* {?}

Reinfelder, J. R. & N. S. Fisher. 1991. The assimilation of elements ingested by marine copepods Science 251: 794-796. *[Acartia tonsa, A. hudsonia & Temora assimilation of Ag, Am, C., Cd, P. S, Se & Zn (27%)]*

Roman, M. R. 1985. Utilization of detritus by the copepod Acartia tonsa. Limnol. Oceanogr. 29: 949-959. *[Detritus insufficient for egg-to-adult development, but Acartia can use detritus to supplement its diet]* {11}

Roman, M. R. and A. L. Gauzens. 1997. Copepod grazing in the equatorial Pacific. Limnol. Oceanogr. 42: 623-634. *[Copepods can control diatom abundances in Oct. but not in March/April during El Nino conditions. Most copepod fecal*

pellets ingested within euphotic zone and most carbon is from protozoans, not phytoplankton. Fraction of primary production consumed by copepods around the world tabulated.] {?}

Rublee, P. A. & C. L. Gallegos. 1989. Use of fluorescently labeled algae (FLA) to estimate microzooplankton grazing. Mar. Ecol. Prog. Ser. *51*: 221-227. *[Why bother? Algae come with their own fluorescent tags: photosynthetic pigments]*[**8**]

Runge, J. A. 1985. Relationship of egg production of *Calanus pacificus* to seasonal changes in phytoplankton availability in Puget Sound, Washington. Limnol. Oceanogr. 30: 382-396. *[Lab studies used to find hyperbolic relation between food and egg production, which was then applied to the field]*

Runge, J. A. & M. D. Ohman. 1982. Size fractionation of phytoplankton as an estimate of food available to herbivores. Limnol. Oceanogr. *27*: 570-576. *[Phytoplankton are filtered through various filters to demonstrate the availability of food for copepods. Knowing the concentration of chl a is not enough for estimating food supply for grazers]*

Sterner, R. W. 1986. Herbivores direct & indirect effects on algal populations. Science *231*: 605-607. *[Zooplankton can enhance as well as inhibit phytoplankton growth]*

Stoecker, D. K., T. L. Cucci, E. M. Hurlbert, & C. M. Yentsch. 1986. Selective feeding by *Balanion* sp. (Ciliata: Balanionidae) on phytoplankton that best support its growth. J. exp. Mar. Biol. Ecol. *95*: 113-130. *[Copepods aren't the only grazers & in many environments the microzooplankton may be the dominant grazers]* [**4**]

Tremaine, S. C. & A. L. Mills. 1987. Tests of the critical assumptions of the dilution method for estimating bacterivory by microeucaryotes. Appl. env. Micro. *53*: 2914-2921. [**7**]

Turner, J. T. & P. A. Tester. 1989. Zooplankton feeding ecology: nonselective grazing by the copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, & *Eucalanus pileatus* Giesbrecht in the plume of the Mississippi River. J. exp. Mar. Biol. Ecol. *126*: 21.

Turner, J. T. & P. A. Tester. 1997. Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. Limnol. Oceanogr. 42: 1203-1214. *[Review of known phytoplankton toxins, their ingestion by zooplankton, the effects on zooplankton and potential for trophic transfer]*

Vanni, M. J. 1987. Effects of nutrients & zooplankton size on the structure of a phytoplankton community. Ecology *68*: 624-635.

Verity, P. G. 1986. Grazing of phototrophic nanoplankton by microzooplankton in Narragansett Bay. Mar. Ecol. Prog. Ser. *29*: 105-115. *[62% of primary production goes to microzooplankton.]*

Vidal, J. 1980. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, & body size on the growth rate of *Calanus pacificus* & *Pseudocalanus* sp. Marine Biology *56*: 111-134. 2. Effects of phytoplankton concentration, temperature, & body size on the development & molting rates of *Calanus pacificus* & *Pseudocalanus* sp. Ibid: 135-146. 3. Effects of phytoplankton concentration, temperature, & body size on the metabolic rate of *Calanus pacificus*. Ibid: 195-202. IV. Effects of phytoplankton concentration, temperature, & body size on the net production efficiency of *Calanus pacificus*. Ibid: 203-211. *[Vidal's tour de force was the complete documentation of the growth rates of the two most important microzooplankton taxa on the west coast.]*

Welschmeyer, N. A. & C. J. Lorenzen. 1985. Chlorophyll budgets: zooplankton grazing & phytoplankton growth in a temperate fjord & the Central Pacific gyre. Limnol. Oceanogr. *30*: 1-21. *[Following Shuman's discovery that Chl a is stoichiometrically converted to pheophorbide a in copepod guts, W & S balance the water-column grazing budget, calculating the relative importance of macro- & microzooplankton grazing.]* [**4**, **26**]

White, J. R. and M. R. Roman. 1992. Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. Mar. Ecol. Prog. Ser. *86*: 251-261. *[Primary production dominated by large cells and grazing by mesozooplankton; cited by **Nagata 2000**]* [?]

Wilson, D. S. 1973. Food size selection among copepods. Ecology *54*: 909-914. *[A key paper in the debate whether copepods use leaky sieves {they don't} He tested the hypothesis with glass spheres.]*

ARE COPEPODS FOOD-LIMITED?

Huntley, M. D. and C. Boyd. 1984. Food-limited growth of marine zooplankton. Amer. Natur. 124: 455-478. *[Existing data are modeled, and they conclude that coastal populations of zooplankton appear to not be food-limited but oceanic populations are probably food-limited.]* {?}

Huntley M. D. and M. G. D. Lopez. 1992. Temperature-dependent production of marine copepods: a global synthesis. Amer. Natur. 140: 201-242. *[A single function is used to fit the growth of copepods from egg to adult as a function of temperature. Since lab growth rates under food-satiated conditions appear similar to field rates, they argue, as did* ***McLaren (1978)*** *that copepods may not be food-limited.* ***Miller (2004)*** *reviews their model and the ensuing controversy]* {**8**}

Kleppel G. S., C. S. Davis, and K. Carter. 1996. Temperature and copepod growth in the sea: a comment on the temperature-dependent model of Huntley & Lopez. Amer. Natur. 148: 397-406. *[The argue that copepod growth rates may be much lower than temperature-controlled optima due to food limitation] {?}*

McLaren, I. A. 1978. Generation lengths of some temperate marine copepods: estimation, prediction, & implications. J. Fish. Res. Board Can. *35*: 1330-1342. *[Since development times in the field are similar to lab development times under food satiated conditions, copepods may not be food limited in nature. The generation times of calanoid copepods in the field are close to the shortest generation times expected based on laboratory studies of copepods growing at those field temperatures & saturating food densities.* ***Huntley & Lopez (1992)*** *extend this argument.]*[**8**, **31**]

THE DILUTION METHOD

Comment: *Landry & Hassett (1982) introduced the dilution method to biological oceanography. It is now a major method for estimating the taxon-specific specific growth rate (μ) and grazing rate. Gallegos and Vant (1996) use the dilution method to estimate C:Chl a ratios.*

Båmstedt, U., D. J. Gifford, X. Irigoien, A. Atkinson, and M. Roman. 2000. Feeding. Pp. 297-399 *in* R. Harris, P. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley, eds., ICES Zooplankton Methodology Manual. Academic Press, San Diego. 684 pp. *[This is the best available compilation of methods, including the dilution method]*

Gallegos, C. L. and W. N. Vant. 1996. An incubation procedure for estimating carbon-to-chlorophyll ratios and growth irradiance relationships of estuarine phytoplankton. Mar. Ecol. Prog. Ser. *138*: 275-291. *[The dilution method is used with ^{14}C incubations to estimate C:Chl a ratios.]*

Landry, M. R. & R. P. Hassett. 1982. Estimating the grazing impact of marine microzooplankton. Marine Biology *67*: 283-288. *[The dilution method introduced]* [**7**]

Landry, M. R. J. Constantinous, & J. Kirshtein. 1995a. Microzooplankton grazing in the equatorial Pacific during February & August 1992. Deep-Sea Res. *42*: 657-672.

Landry, M. R., J Kirshtein & J. Constantinou. 1995b. A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental tests in the central equatorial Pacific. Mar. Ecol. Prog. Ser. *120*: 53-63.

Pigment- & taxon-specific dilution method

Burhill, P. H., R. C. F. Mantoura, C. A. Llewellyn & N. J. Powers. 1987. Microzooplankton grazing & selectivity of phytoplankton in coastal water. Mar. Biol. *93*: 581-590. *[Specific growth rates for each group of phytoplankton calculated.]*[**7**]

Latasa, M, M. R. Landry, L Schlülter & R. R. Bidigare. 1997. Pigment-specific growth & grazing rates of phytoplankton in the central equatorial Pacific. Limnol. Oceanogr. *42*: 289-298. *[Dilution experiments during & after an El Niño event Microzooplankton control the slow growing prymnesiophytes & prochlorophytes, but not the diatoms]*[**7**]

Strom, S. L. & N. A. Welschmeyer. 1991. Pigment-specific rates of phytoplankton growth & microzooplankton grazing in the open subarctic Pacific Ocean. Limnol. Oceanogr. *36*: 50-63. *[48-h, clean bottle, incubations with dilution grazing experiments & pigment-specific μ determinations (by HPLC). Highest growth rates for diatoms, with the highest grazing rates on small cells]*[**7**]

Waterhouse, T. T. and N. A. Welschmeyer. 1995. Taxon-specific analysis of microzooplankton grazing rates and phytoplankton growth rates. Limnol. Oceanogr. 40: 827-834. *[Dilution method adapted to estimate change in taxon-specific pigments. 21-55% of primary production in Monterey Bay consumed by microzooplankton]* {**4**, **7**}

NOVEL GRAZING (HETEROTROPHIC DINOFLAGELLATES)

Hansen, P. J. 1991. Dinophysis: a planktonic dinoflagellate genus which can act both as a prey & a predator. Mar. Ecol. Prog. Ser. *69*: 201.

Jacobson, D. M. & D. M. Anderson. 1986. Thecate heterotrophic dinoflagellates: feeding behaviour & mechanism. J. Phycology *22*: 249.

Lessard, E. J. 1991. The trophic role of heterotrophic dinoflagellates in diverse marine environments. Marine Microbial Food Webs *5*: 49.

Suttle, C. A., A. M. Chan, W. D. Taylor, & P. J. Harrison. 1986. Grazing of planktonic diatoms by microflagellates. J. Plankton Res. *8*: 393-398.

TOXIC DIATOMS?

Ban SH, Burns C, Castel J, Chaudron Y, Christou E, Escribano R, Umani SF, Gasparini S, Ruiz FG, Hoffmeyer M, Ianora A, Kang HK, Laabir M, Lacoste A, Miralto A, Ning XR, Poulet S, Rodriguez V, Runge J, Shi JX, Starr M, Uye S, Wang YJ. 1997. The paradox of diatom-copepod interactions. Mar. Ecol. Prog. Ser. 157: 287-293. *[Abstract: "Here, 15 laboratories located worldwide in 12 different countries and representing a variety of marine, estuarine and freshwater environments present strong evidence that diatom diets are in fact inferior for copepod reproduction. When fed to females of 16 copepod species, all but 1 of the 17 diatoms examined significantly reduced egg production rates or egg viability compared to non-diatom controls. "]* {**8**}

Irigoien, X., R. P. Harris, H. M. Verheye, P. Joly, J. Runge, M. Starr, D. Pond, R. Campbell, R. Shreeve, P. Ward, A. N. Smith, H. G. Dam, W. Peterson, V. Tirelli, M. Koski, T. Smith, D. Harbour, R. Davidson. 2002. Copepod hatching success in marine ecosystems with high diatom concentrations. Nature 419: 387-389. *[There is no apparent correlation between field hatching success and diatom abundance. Field populations may select other food or supplement a diatom diet with flagellates]* {**8**}

Kleppel G. S., D. V. Holliday, and R. E. Pieper. 1991. Trophic interactions between copepods and microplankton: a question about the role of diatoms. Limnol. Oceanogr. 36: 172-178. *[Copepods feed preferentially on dinoflagellates & microzooplankton, not diatoms. Egg production uncorrelated with diatom abundance]* {?}

Miralto A., G. Barone, G. Romano, S. A. Poulet, I. Ionara, G. L. Russo, I. Buttino, G. Mazzarella, M. Laabir, M. Cabrini, and M. G. Giacobbe . 1999. The insidious effect of diatoms on copepod reproduction. Nature 402: 173-176. *[Only 12% of eggs produced during a diatom bloom hatch, and a toxic aldehyde is implicated]* {**8**}

ACARTIA'S OMNIVORY

Barnett, A. M. & A. E Jahn. 1987. Pattern & persistence of a nearshore planktonic ecosystem off Southern California. Cont. Shelf Res. 7: 1-25. *[Cluster analysis (UPGA sorting of correlations) is used to group zooplankton sampled in offshore transects. Barnacle larvae, Oithona, & Acartia dominate inshore; the offshore is dominated by Calanus pacificus, Eucalanus californicus, & Rhinocalanus.]*

Berggreen, U., B. Hansen, & T. Kiørboe. 1988. Food size spectra, ingestion & growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Marine Biology *99*: 341-352. *[Egg production rates can be used to infer past feeding history.]*

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Gifford, D. J. & M. J. Dagg. 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana: Carnivory vs. herbivory in natural microplankton assemblages. Bull. Mar. Sci. *43*: 458-468. [**11**, **12**]

Heinle, D. R., R. P. Harris, J. F. Ustachi & D. A. Flemer. 1977. Detritus as food for estuarine copepods. Marine Biology *40*: 3412-353. [**11**, **13**]

Jonsson, P. R. & P. Tiselius. 1990. Feeding behavior, prey detection & capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. Mar. Ecol. Prog. Ser. *60*: 35-44.

Kiørboe, T, E. Saiz, & M. Viitasalo. 1996. Prey switching behaviour in the planktonic copepod Acartia tonsa. Mar. Ecol. Prog. Ser. *143*: 65-75. *["A. tonsa has 2 different prey encounter strategies. It can generate a feeding current to encounter & capture immobile prey (suspension feeding) or it can sink slowly & receive motile prey by means of mechanoreceptors on the antennae (ambush feeding). Acartia feeds on ciliates. Ciliates may peak during diatoms blooms, because Acartia predation is less then.]*

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Stoecker, D. K. & D. A. Egloff. 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates & rotifers. J. exp. mar. Biol. Ecol. *110*: 53-68. *[A key paper showing that this supposed herbivore is an omnivore]*[**12**, **24**]

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Turner, J. T. 1984. Zooplankton feeding ecology: contents of fecal pellets of the copepods *Acartia tonsa* & *Labidocera aetiva* from continental shelf waters near the mouth of the Mississippi River. P. S. Z. N. I. Mar. Ecol. 5: 265-282. *[Acartia is herbivorous]*[**11**, **13**]

Turner, J. T. 1994. Planktonic copepods of Boston Harbor, Massachusetts Bay & Cape Cod Bay. Hydrobiologia *292/293*: *405-413. [Turner, with MWRA funding, documents the seasonal & spatial variation in zooplankton abundance. Copepods dominate biomass, with the small copepod Oithona similis, & Paracalanus parvus dominating biomass. Other dominant copepods are Pseudocalanus newmani, Temora longicornis, Centropages hamatus. C. typicus & Calanus finmarchicus. Two species of Acartia, A. tonsa & A. hudsonica, were abundant in Boston Harbor with Eurytemora hermani as a subdominant. Oithona similis may feed primarily as a carnivore. Calanus finmarchicus, an important food item for endangered right whales, is unlikely to be affected by 'trophic domino effects'.]*

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Yen, J. 1985. Selective predation by the carnivorous marine copepod *Euchaeta elongata*: laboratory measurements of predation rates verified by field observations of temporal & spatial feeding patterns. Limnol. Oceanogr. *30*: 577-597.

Sloppy Grazing

Jumars, P. A., D. L. Penry, J. A. Baross, M. J. Perry & B. W. Frost. 1989. Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion & absorption in animals. Deep-Sea Res. *36*: 483-495. *[The source of DOM, fueling the microbial loop may be from inefficient (but optimal) grazer guts]*

Nagata. T. 2000. Production mechanisms of dissolved organic matter. Pp. 121-152 *in* D. L. Kirchman, ed, Microbial ecology of the oceans. Wiley-Liss, New York. 542 pp. [31]

Strom, S. L, R. Benner, S. Ziegler, & M. J. Dagg. 1997. Planktonic grazers are a potentially important source of marine dissolved organic matter. Limnol. Oceanogr. *42*: 1364-1374.

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Holling, C. S. 1959. The components of predation as revealed by a study of mall-mammal predation of the European Pine Sawfly. Canadian Entomologist *91*: 293-320. *[A study of the number of insect cocoons opened per rodent vs. cocoon density is used as a springboard to describe the Type 1→ 4 functional response curves. The type 4 response curve is just a modified Type 3 (sigmoid) response curve. Combined with the 3 major functional responses are 3 numerical responses: direct, inverse, & none]*[2, 9, 20, 27, 28]

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Stephens, D. W. & J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton NJ 247 pp. *[An outstanding review— no marine examples though]*

Miscellaneous

Vogel, S. 1981. Life in moving fluids. The physical biology of flow. Princeton University Press, Princeton, N. J. [5]

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