ECOS 630 Biol. Ocean. Processes Chapter 20 Gallagher home Revised: 11/18/08 ©2008 E. D. Gallagher

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SIZE- SELECTIVE PREDATION AND COMPETITION

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Assignment

REQUIRED

Brooks, J. L. and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

SUPPLEMENTAL

- Briand, F. and E. McCauley. 1978. Cybernetic mechanisms in lake plankton systems: how to control undesirable algae. Nature 273: 228-230. [Levins' Loop analysis is applied to lake systems. Some simple predictions are verified using loop diagrams. Despite their comment in the text that the model is sign-stable, their simple model contains a 3-cycle and cannot be sign stable. The predictions are ambiguous.]
- Greene, C. H. 1983. Selective predation in freshwater zooplankton communities. Int. Revue ges. Hydrobiol. 68: 297-315. [A review of the effects of invertebrate and visually feeding predators]
- Kerfoot, W. C. 1975. The divergence of adjacent populations. Ecology 56: 1298-1313. [Size composition of <u>Bosmina</u> <u>longirostris</u> populations on the shore and open water of Lake Union are controlled by different intensities of vertebrate and invertebrate predation.]
- Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. [Read pp. 162-178 on zooplankton life history & mortality rates]
- Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826.
- Paine, R. T. 1966. Food web complexity and species diversity. Amer. Natur. 100: 493-532. [Increased predation leads to increased diversity. Later modified by Connell to the intermediate disturbance hypothesis]

Comments on the Readings

To what extent is marine ecosystem structure determined by physical forces and nutrient flux from below *vs.* control by top-level predators? This question has been debated for at least the last 25 years and is now referred to as the "bottom-up" or "top-down" dichotomy. One "top-down" control hypothesis is called the predator or trophic-cascade hypothesis: control at higher trophic levels has cascading effects on lower trophic levels. By changing the type or quantity of predation at the highest levels in an aquatic ecosystem, one can change the quantity, size or species composition of the phytoplankton. In bottom-up control, nutrient supply is the overwhelmingly important factor controlling phytoplankton standing stocks. **Brett & Goldman**



(1997) recently reanalyzed eleven nutrient and predator manipulation experiments, finding that nutrient supply does have the major effect on phytoplankton biomass, but that top predators do have a strong influence on zooplankton biomass.

The required papers for today's class are classics. **Brooks & Dodson (1965)** describe a survey of fish and zooplankton in Connecticut lakes carried out in 1942, 1962 and 1964. In some of the lakes, planktivorous (plankton eating) fish were introduced 10 years prior to the 1964 sampling. **Brooks & Dodson (1965)** proposed the size-efficiency hypothesis to explain the difference in size structure between lakes with and without fish. This size-efficiency hypothesis has five parts:

- 1. Planktonic herbivores all compete for the fine particulate matter (1-15 μ m)
- 2. Larger zooplankton do so more efficiently and can also take larger particles.
- 3. When predation is of low intensity the small planktonic herbivores will be competitively eliminated by large forms (dominance by large Cladocera and calanoid copepods)
- 4. But when predation is intense, size-dependent predation will eliminate the large forms, allowing the small zooplankton (rotifers, small Cladocera) that escape predation to become dominant.
- 5. When predation is of moderate intensity, it will, by falling more heavily upon the larger species, keep the populations of these more effective herbivores sufficiently low so that slightly smaller competitors are not eliminated.

The size-efficiency hypothesis (SEH) is one of the most important hypotheses proposed in aquatic science. However, this bold hypothesis is not an adequate explanation of the changes in planktonic size structure even in Connecticut Lakes. The hypothesis predates and subsumes R. T. Paine's more well-known (1966) keystone predation hypothesis. Parts of the SEH, particularly the negative association between large zooplankton and fish, were confirmed by Reif & Tappa (1966), Galbraith (1967) and Wells (1970). Zaret (1972) and Kerfoot (1975) broadened the concept to include changes in zooplankton phenotypes being controlled by visual predators. Zaret (1972) studied zooplankton in Lake Gatun in Panama, and Kerfoot studied



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phytoplankton cells (part 2 of the S-E hypothesis).

The size-efficiency hypothesis has been criticized, and no part of the hypothesis is strictly correct. Hall et al. (1970) and Neill (1975a) showed that small zooplankton can outcompete larger zooplankton. Further, Neill (1975b) showed that there was a great deal of resource partitioning of phytoplankton on the basis of size (*i.e.*., part a) of the size-efficiency hypothesis was not universal). **Dodson (1974b)** failed to find competitive exclusion between large and small zooplankton in the field. Bengtssen (1987a & b) reviewed both laboratory and field evidence that tested the hypothesis that large zooplanktonic grazers were competitively superior, concluding that large zooplankton are often, but not always, the superior competitor in laboratory and field experiments (18 of 30 experiments & 8 of 10 field experiments).

The key modification of the size-efficiency hypothesis was the discovery of the importance of invertebrate predators. Often, the major prey consumed by visually feeding fish are themselves carnivorous. Many of the large zooplankton that **Brooks & Dodson (1965)** had assumed to be





of the effect of visual predators on vertical migration patterns. Gliwicz's (1986) is on the reading list for the next class on vertical migration. Figure 1 summarizes Brooks & **Dodson's (1965)** view of the role of visually feeding predators in aquatic

systems. Visually feeding fish feed selectively on the larger zooplankton. Large and small zooplankton compete for medium-sized phytoplankton cells. Brooks & **Dodson (1965)** hypothesized that large zooplankton grazers would be the superior competitors because they could ingest large

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grazers were predators on smaller zooplankton. Figure 2 shows a more realistic view of the role of visually feeding predators in aquatic systems. Competitive dominance by large copepods does not need to be invoked to explain the change to smaller zooplankton after the introduction of fish. Dodson (1970, 1974b) introduced the central importance of invertebrate predators in



Marine zooplankton ecologists were relatively slow in applying the size-

efficiency hypothesis to marine communities. **Rakusa-Suszcewski (1969)** was one of the first to document the highly size-selective feeding by marine chaetognaths on their calanoid copepod prey. Larger chaetognaths prey on larger (and older) calanoid copepods.

effectively on large prey. Fish, and other visually feeding

predators, feed selectively on large prey.

Steele & Frost (1977) modeled the cascading top-down effects of vertebrate and invertebrate predators on zooplankton and phytoplankton community structure, a concept later picked up by Carpenter *et al.* (1985, 1987), who do not cite the earlier Steele & Frost (1977) model. Carpenter et al. (1985) proposed the trophic cascade model: the addition of piscivorous (fisheating) fish leads to a decrease in planktivorous fish, which leads to an increase in large zooplankton, which leads to a decrease in phytoplankton. DeMello *et al.* (1992) critically reviewed the data supporting the hypothesis and found that the coupling between top predators



and phytoplankton abundance wasn't general, depending on the prevalence of intermediate trophic links including the importance of invertebrate predation.

Gerritsen & Strickler (1977), Pastorek (Ph.D. dissertation & 1981), and later C. Greene (1983, 1986, 1988) produced models, both verbal and mathematical, to describe prey detection by marine predators. Jeannette Yen (1982, 1985) showed that there was intense invertebrate predation on smaller marine calanoid copepods. Yen studied the large predatory calanoid copepod *Euchaeta*, shown in Fig. 3. Yen's findings were confirmed by Greene & Landry (1985). Ohman (1988, 1990) clearly demonstrated that predation controlled the abundance and phenotype (e.g., vertical migration mode) of Pseudocalanus in Dabob Bay.

Neill (1975a) is one of the finest studies of

flaw: it is a laboratory study. L. C. Birch, the noted calanoid copepod that detects calanoid prey Australian insect ecologist and more noted critic of by mechanoreception (photographed by competition theory, is reputed to have said,



competition ever published. It has only one notable Figure 3. Euchaeta elongata, a predatory Jeanette Yen). The long, grasping 2^{nd} "Competition occurs, but not in Nature." Neill also maxillae are visible.

criticized competition theory. In his first published paper on these laboratory data, Neill (1974) showed that competition among microcrustacean could not be adequately modeled using the Lotka-Volterra competition equations, because of higher order interactions.

Neill's (1975a) study should be viewed as a study of the effects of competition among zooplankton if resources (phytoplankton) are limiting. Neill's (1975a) study clearly demonstrated intense competition between zooplankton species and zooplankton developmental stages for size classes of phytoplankton. Neill (1975a) introduced the "bottleneck hypothesis" that states that the growth of a population can be limited by competitive interactions that affect only one developmental stage of a species and that ramify through subsequent stages. In his experiments, Daphnia magna was competitively excluded from the microcosms because its developmental stages could not survive competition with *Ceriodaphnia*. Neill (1975a) was able to produce superb life tables for each of the species, a remarkable accomplishment in itself.

Carpenter et al. (1985, 1987) proposed the trophic-cascade or predator cascade hypothesis. This hypothesis states that the size structure of a community can be set by the top-level predators. In the cascade model, as fish predation intensity increases, the planktivore density decreases, herbivores increase and Chl a decreases. Steele and Frost (1977) had shown this pattern with a simulation model a decade earlier. McQueen et al. (1989) proposed an alternate hypothesis, which he called the "bottom up:top down model", in which Chl a is independent of fish abundance. Mazumder et al. (1990) and Murtaugh (1989) provide other analyses on the effects of fish on the size composition of lakes.



O'Brien (1979) and **Greene (1983)** summarized the mechanisms used by visually feeding predators to ingest prey. The probability of ingestion, $_{\Pi}$ can be computed from the following conditional probabilities:

Probability of Ingestion (P_I) : $P_I = P_L \times P_P \times P_A \times P_C$.where, $P_I = Probability$ of ingestion. $P_L = Probability$ of locating prey = $P_E = P$ (encounter). $P_P = Probability$ of pursuit $P_A = Probability$ of attack $P_C = Probability$ of capture.

P_L can be computed from the reactive distance of a visually feeding fish and is a strong linear function of light intensity and prey size (mm). **O'Brien's (1979)** model, involving spherical reactive volumes, indicate that a 2-mm *Daphnia* is 27 times more likely to be eaten as a 1-mm length *Daphnia*. **Gerritsen & Strickler (1977)** showed that the Probability of encounter is dependent on both predator and prey density and the swimming speeds of predator and prey and the encounter volumes. Invertebrate predators can be divided into cruising (*e.g.*, some cyclopoid copepods) and ambush predators (*e.g.*, *Chaoborus*) based on their motility while encountering prey. In general, ambush predators tend to encounter the larger, more rapidly swimming prey items.

The probability of pursuit, given location is generally close to 1.0, in that fish rarely fail to pursue a located prey. Some exceptions involve prey that are toxic, and some prey are brightly colored to signify their unpalatability (Kerfoot (1982) has described the behavioral interactions involving an unpalatable, brightly colored mite, which is "Better red than dead".)

The probability of attack depends on the mechanism of ingestion, which can include sucking, filtering (*e.g.*, through gill rakers), or pump filtering. Copepods can evade some pumpers. The probability of capture can sometimes be affected by the spacing between gill rakers in fish.

There are a variety of adaptations, both physiological and genetic for reducing predation mortality. These include escape responses, armored exoskeletons, large body size, deadman sinking responses, and reverse diel vertical migration to avoid invertebrate predation. Adaptations in response to visually feeding predators include diel vertical migration, small size, lateral compression, and invisibility. There are often large demographic costs associated with adaptations to reduce predation mortality, especially invertebrate mortality. Larger adult size is often associated with a delayed age to first reproduction. Armoring is associated with reduced fecundity (Kerfoot 1977).

NATURAL SELECTION OF PREDATOR DEFENSE: KAIROMONES



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Kairomones are chemicals released by the action of one organism that have no effect on that organism but affect the behavior or physiology of another. Both the behavior and morphology of freshwater and marine zooplankton populations change in response to the presence of invertebrate and invertebrate predators. Cyclomorphosis is the change in morphology seasonally, noted especially in freshwater daphnid populations. Figure 4 shows the change in morphology of cladocera observed in a lake system. The large helmeted morph is more resistant to invertebrate predation than the normal morph. Agrawal et al. (1999) document 'transgenerational induction' of predator defense. If a mother brooding eggs, late in their development, is exposed to kairomone (an as yet unknown chemical) from either of the major invertebrate predators of this species, the young will develop helmets even if they were born and raised in a kairomone-free medium. If the kairomone is added only during the early stages of egg development, the eggs develop into the normal morph. This behavior is not evidence for Lamarckian selection, as it is a physiological response, not genetic. Beaton & Hebert (1997) document that the expression of different cell types is altered by the presence of the kairomone during development.



Figure 4. Cyclomorphosis in a clone of *Daphnia cucullata*. Both morphs are genetically identical, but the helmeted morph (left) is produced in response to a kairomone produced by the predatory cladoceran *Leptodora* or the predatory phantom midge larva *Chaoborus*. Figure from Agrawal et al. (1999)



Kairomones from fish induce vertical migration behavior in freshwater and marine zooplankton populations. **Davidowicz & Loose (1992)** provide a remarkable demonstration of the phenomenon. Clones of Daphnia, the freshwater cladoceran were isolated and grown in columns. When kairomone from fish was dripped in the medium, the clones exhibited a phenomenal vertical migration pattern, as shown in Figure 5.

MNEMIOPSIS & THE DESTRUCTION & RECOVERY OF THE **BLACK SEA**

Kideys (2002) and Finenko et al. (2003) document the remarkable story of the destruction of the Black Sea and its remarkable recovery due to the predatory effects of two ctenophores. In the early 1980s, the ctenophore (or "comb jelly") *Mnemiopsis leidyi*, common on the East coast of the United States including Narragansett Bay and Boston Harbor, was introduced into to the Black Sea by accident. It is a

voracious predator on zooplankton and fish. *Mnemiopsis* reduced the pelagic prey of the dominant fish in the black sea, the anchovy, and preyed on anchovy larvae. In 1997, another ctenophore appeared in the North Sea, and this ctenophore *Beroe* was a predator of *Mnemiopsis*, see Figure 6. Within a year, the *Beroe* had reduced *Mnemiopsis* abundances to low levels and the zooplankton and fish stocks had begun to recover.



Fig. 2. Swimming tracks of the *Daphnia* individuals in the no-fish treatment (above) and in the fish treatment (below) in the stratification experiment, Thick lines reflect the average population depth. The day/ night cycle is indicated by the bars at the top of the panels.





Invading the invader. (Bottom) The arrival of the Northwestern Atlantic ctenophore (comb jelly) *Mnemiopsis* in the Black Sea via the ballast waters of cargo ships in the early 1980s devastated the natural ecosystem of this marine environment. (Top) *Beroe* species of ctenophore are the natural predators of *Mnemiopsis*. The arrival of *Beroe* in the Black Sea in 1997 resulted in control of the *Mnemiopsis* population and contributed to recovery of the Black Sea ecosystem. In this photograph, a *Beroe* ctenophore has ingested the smaller *Mnemiopsis*, which is visible inside its gut cavity.

Figure 6. *Beroe* ingesting a *Mnemiopsis* from Kideys (2002)

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Outlines of papers

REQUIRED

Brooks, J. L. and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.[3, 4]

- 1. Survey of Connecticut lakes.
 - a. Large cladoceran, *Daphnia*, not found in lakes containing *Alosa*
 - b. Sampled in 1942, 1962, and 1964
 - c. Alosa became established in Crystal Lake in 1955.
 - i. 1942 survey: pre-fish
 - ii. 1964: about 1 decade after fish



Figure 7. Brooks & Dodson (1965) Figure 4.

- d. Size-efficiency hypothesis.
 - i. Planktonic herbivores all compete for the fine particulate matter (1 to $15 \,\mu$ m)
 - ii. Larger zooplankters do so more efficiently and can also take larger particles.
 - iii. When predation is of low intensity the small planktonic herbivores will be competitively eliminated by large forms (dominance of large Cladocera and calanoid copepods)
 - iv. But when predation is intense, size-dependent predation will eliminate the large forms, allowing the small zooplankters (rotifers, small cladocera) that escape predation to become the dominants.
 - v. When predation is of moderate intensity, it will, by falling more heavily upon the larger species, keep the populations of these more effective herbivores sufficiently low so that slightly smaller competitors are not eliminated.





SUPPLEMENTAL

Greene, C. H. 1983. Selective predation in freshwater zooplankton communities. Int. Revue ges. Hydrobiol. 68: 297-315. [A review of the effects of invertebrate and visually feeding predators]



Figure 7. Green Figure 1.



Figure 7. Green Figure 2.

	Vertebrate Predators	ertebrate Invertebrate Predators Predators Ambush Cruising	
Sensory Cues	Visual	Mechanical	Mechanical
Encounter Factics	Cruising	Sit and Wait	Cruising
Strike Factics	Buccal Suction	Grasping	Grasping
Relative Size Ratio Predator/Prey)	Large	Low to Intermediate	Low to Intermediate
Relative Capture Success	High	Low to Intermediate	Low to Intermediate

Figure 7. Green Table 1





Table 2. Prey strategies to reduce vulnerability to predation					
ĺ	Precontact (eg., copepods)	Postcontact (eg., rotifers, cladocerans)			
Encounter Avoidance Strategies	Habitat Segregation: vertical migration Reduced Swimming Speed Reduced Hydrodynamic Perceptibility Reduced Visibility: reduced size, pigmentation, motion				
Strategies to Reduce Susceptibility	Behavioral: escape response	Behavioral: "dead man response" spiralling escape trajectories Morphological: reinforced integument spines and helmets (cyclomorphosis)			

Figure 7. Green Table 2.

Kerfoot, W. C. 1975. The divergence of adjacent populations. Ecology 56: 1298-1313. [Size composition of <u>Bosmina longirostris</u> populations on the shore and open water of Lake Union are controlled by different intensities of vertebrate and invertebrate predation.]

Neill, W. E. 1975a. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826.

Conclusions:

- a. In controls, *Ceriodaphnia* competed with the young of other planktonic species for smaller cells. Increased juvenile survivorship and earlier ages of first reproduction indicated that the young animals are able to get more resources under predation conditions.
- b. The prolongation of adult life in (several larger species) despite improved juvenile survivorship indicated conditions for adults were worse in communities with reduced predation.
- c. Age-specific competition for limited resources implies that bottle-necks in the life cycles of these species could have readily affected the efficiency with which given resources were exploited and the number of species that were supported.





Figure 7. Neill Figure 1







Figure 7. Neill Figure 2



Figure 7. Neill Figure 3





Figure 7. Neill Figure 4

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PREDATION

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- Banse, K. R. 1990. Mermaids their biology, culture, and demise. Limnol. Oceanogr. 35: 148-153. [A tongue-in-cheek review of the extinction of mermaids, caused by the man-induced increased in 'stinging' gelatinous zooplankton. This is the text of an address delivered at a festschrift honoring Dr. Banse on his 60th birthday.]
- Bogdan, K. G., J. J. Gilbert. 1984. Body Size and Food Size in Freshwater Zooplankton Proc. Natl. Acad. Sci. USA 81: 6427-6431. [Laboratory tests refute the size-efficiency hypothesis: "We conclude that zooplankton body length may influence the maximal particle size a species can ingest but has little influence on the ingestion of smaller particles. Two frequently used models relating zooplankton body size and food size are unrealistic."]

- Brett, M. T., K. Wiackowski, F. S. Lubnow, A. Mueller-Solger, J. J. Elser, and C. R. Goldman 1994.
 Ecology 75: 2243-2254. [Added different species of grazer and predatory zooplankton in experimental manipulations (all large zooplankton {>83 µm} removed from lake and individual species added), including the raptorial filter-feeding Diaptomus, which is an omnivore feeding on ciliates and phytoplankton. Diacyclops was a carnivore on ciliates]
- Brett, M. T. and C. R. Goldman 1997. Consumer versus resource control in freshwater pelagic food webs. Science 275: 384-386 [Test of top-down, bottom-up control. Meta-analysis of 11 fish-bynutrient factorial plankton community experiments (from the literature). Zooplankton biomas under strong consumer control & phytoplankton was under strong resource control, with moderate impacts o fish. The response of phytoplankton & zooplankton didn't follow Oksanen et al. (1981) theoretical predictions: were the phytoplankton stimulated by N difficult to graze?]
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- Carpenter, S. R. and J. F. Kitchell. 1984. Plankton community structure and limnetic primary production. Amer. Natur. 124: 159-172. [A theoretical model showing how top-down predator control could affect primary production]





- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634-639. [The trophic cascade hypothesis is introduced. Piscivores reduce planktivorous zooplankton, increasing herbivorous zooplankton, reducing phytoplankton and producing increased water clarity] [5, 18]
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He and C. N. von Ende. 1987. Regulation of lake primary productivity by food web structure. Ecology 68: 1863-1876. [Whole-lake manipulations of fish showed that planktivore effects can `cascade down' to affect primary production. The concept is later cited as the `cascading trophic interaction theory', see also McQueen et al. 1989] [?]
- Carpenter, S. R. and P. R. Leavitt. 1991. Temporal variation in a paleolimnological record arising from a trophic cascade. Ecology 72: 277-285 [Pigments from different phytoplankton groups analyzed in stratified sediments. They proposed that the variance in pigment signals should correspond to the maximum lifespan of the dominant predator, a fish (3-5 years). They did find significant variance at 3-5 year scales, confirming their hypothesis]
- Carpenter, S. R. and J. F. Kitchell, eds. 1993. The trophic cascade in lakes. Cambridge Studies in Ecology. Cambridge University Press, New York. [Reports results of whole-lake fish manipulations conducted between 1984 and 1990. Reviewed by Wooten Ecology 75: 2465-2466 (1994)]
- Cerny, M. and J. Bytel. 1991. Density and size distributios of *Daphnia* populations at different fish predation levels. Hydrobiologia 225: 199-208.
- Confer, J. L. and P. I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571-579 [The distance at which fish detect zooplankton is linearly related to length (see also Dodson 1968 for an early documentation of this)]

- Cottingham, K. L. 1999. Nutrients and zooplankton as multiple stressors of phytoplankton communities: evidence from size structure. Limnol. Oceanogr. 44: 810-827. [Increased P loading & zooplankton size lead to larger phytoplankton and negative effects on the abundance of small phytoplankton]
- Crowl, T. A. and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. Science 247: 949-951. [Crayfish predation causes delayed snail maturity]
- Currie, D. J., P. Dilworth-Christie, and F. Chapleau. 1999. Assessing the strength of top-down influences on plankton abundance in unmanipulated lakes. Can. J. Fish. Aquat. Sci. 56: 427-436.
- Dagg, M. J. 1974. Loss of prey body content during feeding by an aquatic predator. Ecology 55: 903-906. [Some predators are inefficient foragers, losing more than 50% of the labile organic matter in prey. This paper was before its time. Jumars et al. 1989 consider the ecological importance of inefficient grazing in general. Such 'sloppy' feeding may fuel the microbial loop.]
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- DeMello R., R. France, and D. J.McQueen. 1992.
 Biomanipulation: hit or miss? Limnol.
 Oceanogr. 37: 192-207. [Lake biomanipulation theory proposes that increased piscivore abundance will lead to decreased zooplankton predation, increased zooplankton herbivory, decreased phytoplankton abundance and increased water clarity. Data from 50 papers describing 44 lake manipulations are examined critically. Of 118 predictions, 52 were consistent with biomanipulation theory, 21 inconsistent and 45 undecided. The effect of fish on zooplankton size was very clear, but cascading effects on Chl a was not] [5]



Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15: 131-137. [Dodson sampled 50 ponds from 1965 to 1969; salamanders important in each. Community structure divided into Types A and B. A contains the salamander <u>Ambystoma</u> and smaller herbivores. Type B communities contain larger herbivores and the invertebrate predator <u>Diaptomus</u> <u>shoshone</u>. Of the 15 Type A communities, 13 start as Type B each season.][5]

Dodson, S. I. 1974a. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19: 721-729. [Cyclomorphosis reduces vulnerability to invertebrate predation due to an anti-lock & key mechanism][4]

Dodson, S. I. 1974b. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55: 605-613. [The size-efficiency hypothesis is dead; Long live invertebrate predation!. 12 42-l plankton cages used to show that competition for food not important in controlling herbivore community structure. The predatory copepod Diaptomus shoshone excludes the small herbivore Daphnia minehaha. The evidence for and against the size-efficiency hypothesis is reviewed. Dodson concludes size-selective predation, not size-selective resource competition controls the size structure of these zooplankton communities.][4, 5]

Dodson, S. I. 1979. Body size variations in temperate and arctic zooplankton. Limnol. Oceanogr. 24: 940-949. [Size distributions can be small, large or mixtures. The Hrbáĉek (1958) & Brooks & Dodson (1965) pattern is to have distinct large and small zooplankton assemblages. The shift to large zooplankton in the presence of fish occurs in oligotrophic lakes, but intermediate-sized zooplankton persist if productivity is higher or if the top predator is inefficient.]

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 1999. Fish or jellies a question of visibility?
 Limnol. Oceanogr. 44: 1352-1357. [Two fjords, one dominated by a jelly and the other by a fish, have different water transparencies. The fish don't do well with high light attenuation]
- Eliane, K, D. L. Asknes, M. D. Ohman, S. Wood, and M.B. Martinussen. 2002. Stage-specific mortality of *Calanus* spp. under different predation

regimes. Limnol. Oceanogr. 47: 636-645. [Two different fjords with different predation regimes (invertebrate and vertebrate) sampled, producing drastic differences in stage-specific mortality]

- Elliot, E. T., L. G. Castan~strd, D. Perlmutter, and K. G. Porter. 1983. Trophic-level control of production and nutrient dynamics in an experimental planktonic community. Oikos 41: 7-16. [An interesting paper. Models show that algal standing stocks are highest when the foodwebs are odd length.]
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- Evans, M. S. 1990. Large-lake responses to declines in the abundance of a major fish planktovore- the Lake Michigan example. Can. J. Fish. Aquat. Sci. 47: 1738-1754. [As the alewife declined in '73-'77, large copepods increased and then declined as bloaters, another fish increased]
- Gardner, M. B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. Ecology 62: 571-578. [Experiments with bluegill sunfish indicate fish actively avoid ingesting smaller Daphnia]
- Gerritsen, J. 1984. Size efficiency reconsidered: a general foraging model for free-swimming aquatic animals. Amer. Natur. 123: 450-467. [A theoretical model describing the relative importance of size and swimming speed on vulnerability to predation]
- Gerritsen, J. and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34: 73-82. [Vulnerability to fish predation is a function of size. Larger zooplankton are more likely to be detected and eaten. Large size can offer an escape in size from invertebrate predators.]

Gliwicz, M. Z. 1986. Predation and the evolution of



vertical migration in zooplankton. Nature *320*: 746-748.[**4**]

- Greene, C. H. 1983. Selective predation in freshwater zooplankton communities. Int. Revue ges. Hydrobiol. 68: 297-315. [A wonderful review of the differences between vertebrate and invertebrate predation]
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- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839-928. [Effects of 3 levels of nutrient addition & 2 predator levels tested in experimental ponds. Fish had a strong effect on the size composition of zooplankton]
- Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton populations. Annual Review of Ecology and Systematics 7: 177-208. [A nice review and the introduction of an allometric model on zooplankton growth and mortality.]
- Hambright, K. D. 1994. Morphological constraints in the piscivore-planktivore interaction: implications for the trophic cascade hypothesis. Limnol. Oceanogr. 39: 897-912. [Carpenter et al. (1985) trophic cascade hypothesis tested. Large fish did have strong effects, largely in accord with the trophic cascade hypothesis. Juvenile sunfish fed on invertebrate predators, allowing higher abundance of small herbivorous cladocerans]
- 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]
- Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. ent. Soc. Can. 45: 5-60. [The classic paper introducing Type I, II, and III predatory response curves.]
- Jacobs, J. 1978. Influence of prey size, light intensity, and alternative prey on the selectivity of plankton feeding fish. Verh. Internat. Verein. Limnol. 20: 2461-2466.

- Kerfoot, W. C. 1975. The divergence of adjacent populations. Ecology 56: 1298-1313. [Size composition of <u>Bosmina</u> longirostris populations on the shore and open water of Lake Union are controlled by different intensities of vertebrate and invertebrate predation.] [3]
- Kerfoot, W. C. 1977a. Competition in cladoceran communities: the cost of evolving defenses against copepod predation. Ecology 58: 303-313. [Armor associated with reduced fecundity][7]
- Kerfoot, W. C. 1977b. Implications of copepod predation. Limnol. Oceanogr. 22: 316-325. [Epischura, a predatory copepod, feeds on larger Bosmina and other larger cladocerans. Bosmina populations respond to Epischura predation by becoming armored.]
- Kerfoot, W. C. 1978. Combat between predatory copepods and their prey: Cyclops, Epischura, and Bosmina. Limnol. Oceanogr. 23: 1089-1102. [Predatory copepods aren't clumsy hunters. Cladoceran prey survival results from evolved defensive strategies.]
- Kerfoot, W. C. 1981. Long-term replacement cycles in cladoceran communities: a history of predation. Ecology 62: 216-233. [The seasonal succession from long-featured winter clones of <u>Bosmina</u> to short-featured summer clones is mirrored in lake sediment histories dating to glacial times. Long-featured, <u>Chaoborus</u>-resistant clones replaced by short forms, perhaps due to the introduction of planktivorous fish] {?}
- Kerfoot, W. C. 1982. A question of taste: crypsis and warning coloration in freshwater zooplankton communities. Ecology 63: 538-544. [Many large zooplankton are transparent while others are unpalatable and brightly colored. Better red than dead.] {7}
- Kerfoot, W. C. 1987. Translocation experiments: *Bosmina* responses to copepod predation. Ecology 68: 596-610.
- Lair, N. 1990. Effects of invertebrae predation on the seasonal succession of a zooplankton community: a two year study in Lake Aydat, France. Hydrobiologia *198*: 1-12.





- Landry, M. R. 1977. A review of important concepts in the trophic organization of pelagic ecosystems. Helgol. wiss. Meeresunters. 30: 8-17. [Landry reviews the key differences between invertebrate and vertebrate predators and their effects on mesozooplankton size structure]
- Landry, M. R. 1978. Predatory behavior of a marine copepod, *Labidocera trispinosa*. Limnol. Oceanogr. 23: 1103-1113.
- Landry, M. R. 1980. Detection of prey by *Calanus* pacificus: implications of the first antennae. Limnol. Oceanogr. 25: 545-549.
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- Lonsdale, D. J. 1981. Regulatory role of physical factors and predation for two Chesapeake Bay copepod species. Marine Ecology Progress Series 5: 341-355.
- Lynch, M. 1977. Fitness and optimal body size in zooplankton populations. Ecology 58: 763-774. [Fitness defined in terms of feeding efficiency and vulnerability to predation]
- Lynch, M. 1979. Predation, competition, and zooplankton community structure: an experimental study. Limnol. Oceanogr. 24: 253-272. [In a MN pond, Ceriodaphnia, an intermediate sized cladoceran, is supplanted by a larger cladoceran when Chaoborus predation is intense and by a smaller cladoceran when fish predation is intense]
- Lynch, M. 1980. The evolution of cladoceran life histories. Q. Rev. Biol. 55: 23-42. [Invertebrate predation is a major selective force on cladoceran life histories]
- Lynch, M. 1980. Predation, enrichment, and the evolution of cladoceran life histories: a theoretical approach. Pp 367-376 in W. C. Kerfoot, ed., Evolution and ecology of zooplankton communities. University Press of New England, Hanover, New Hampshire, U.S.A.

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- McLaren, I. A. 1978. Generation lengths of some temperate marine copepods: estimation, prediction, and implications. J. Fish. Res. Board Can. 35: 1330-1342. [Zooplankton are apparently not food-limited (according to I.A.M., anyway). They may be limited by predation. Thus, energetic arguments based on increased food gathering abilities would not work.] {}
- McQueen, D. J. 1990. Manipulating lake community structue: where do we go from here? Freshwater Biology 23: 613-620.
- McQueen, D. J., M. R. S. Johanes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down inputs on freshwater pelagic community structure. Ecol. Monogr. 59: 289-309. [In the Carpenter cascade, a decrease in piscivorous fish leads to an increase in planktivorous fish, a decrease in herbivores and an increase in chl <u>a</u>. In the bottom up/top down concept (which McQueen introduced and supports), chl <u>a</u> concentration is independent of fish abundance.] [?]
- McQueen, D. J, R. France and C. Kraft. 1992. Confounded impacts of planktivorous fish on freshwater biomanipulations. Archiv fur Hydrobiologie 125: 1-24. [A factorial study conducted in large enclosures to assess the effect of nutrients and fish. Fish biomass had no significant effect on chl a concentrations or zooplankton biomass, but there was a significant negative correlation with Secchi depth. This was due to blooms of large algal cells in the fish-free enclosures. In the fish treatement, small phytoplankton cells were more abundant. There was little shift in zooplankton size. As Vanni noted, this may be because of a poor 'species pool' of large zooplankton species. They conclude, 'Because of food web complexity, it is often difficult to distinguish between direct and indirect community effects.'] [?]



Mittlebach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: a long-term whole lake study of predator extinction and reintroduction. Ecology 76: 2347-2360. [Bass removed, planktivorous fish increased, large zooplankton dominated by Daphnia declined. Bass reintroduced and Daphnia reappeared. Fits trophic-cascade hypothesis]

- Murtaugh, P. A. 1981. Size-selective predation on Daphnia by Neomysis mercedis. Ecology 62: 894-900. [Small mysids take small cladocerans and large mysids take large. There is little escape in size from Neomysis]
- Murtaugh, P. A. 1989. Size and species composition of zooplankton in experimental ponds with and without fishes. J. Freshwater Ecology 5: 27-37.
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- O'Brien, W. J., D. Kettle, and H. P. Riesen. 1979. Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. Ecology 60: 287-294. [Alaska lakes with both visual predators and invertebrate predators. Zooplankton adapt to the invertebrate predatros with helmets & armor]
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- Sarnelle, O. 1994. Inferring process from pattern: trophic level abundances and imbedded interactions. Ecology 75: 1835-1841. [Discusses whole lake manipulations of phyto-herbivore-fish]
- Spaak P and J. R. Hoekstra. Fish predation on a hybrid Daphnia species complex: a factor explaining species coexistence? Limnol. Oceanogr. 42: 753-762.[The fitness of hybrids produced by mating two Daphnia species tested. Under strong fish predation, the survival of the larger parental Daphnia was lowest, followed by intermediate survival of the hybrid, in accordance with expectation]
- Steele, J. H. and B. W. Frost. 1977. The structure of plankton communities. Phil Trans. Roy. Soc. London B 280: 485-534. [An ecosystem simulation model, incorporating the effects of phytoplankton and zooplankton grazer size is constructed. Phytoplankton size can be controlled from both bottom-up and top-down factors. For example, changing the top predator to one that feeds on large grazers can lead to a switch to smaller grazer sizes and larger phytoplankton cell sizes.]
- Taylor, B. E. 1980. Size-selective predation on zooplankton. Pp. 377-387 in W. C. Kerfoot, ed., Evolution and ecology of zooplankton communities. University Press of New England, Hanover, New Hampshire, U.S.A.
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community. Can. J. Fish. Aquat. Sci. 45: 1758-1770.

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- Vuorinen, I., M. Rajasilta, and J. Salo. 1983. Selective predation and habitat shift in a copepod species support for the predation hypothesis.
 Oecologia (Berl.) 59: 62-64. [Copepods with egg sacks are more readily detected and eaten.]
- Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556-565. [One of the early confirmations of the size-efficiency hypothesis.][3]
- Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042-1052.
- Wetterer, J. K and C. J. Bishop. 1985. Planktivore prey selection: the reactive field volume model vs the apparent size model. Ecology *66*: 457-464.
- Williamson, C. E. 1993. Linking predation risk models with behavioral mechanisms: identifying population bottlenecks. Ecology 74: 320-331.
- Williamson, C. E., M. E. Stoeckel, and L. G. Schoeneck. 1989. Predation risk and the structure of freshwater zooplankton communities. Oecologia 79: 76-82. [Prey can respond to increased predation by reducing density risk or reducing prey vulnerability]



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- Williamson, C. E. and M. E. Stoeckel. 1990. Estimating predation risk in zooplankton communities: the importance of vertical overlap. Hydrobiologia 198: 125-131.
- Wright, D. I. and W. J. O'Brien. 1984. The development of a field test of a tactical model of the planktivorous feeding of whit crappie (*Pomoxis annularis*). Ecological Monographs 54: 65-98.
- Zaret, T. M. 1972. Predator-prey interaction in a tropical lacustrine ecosystem. 53: 248-257.[3]
- Zaret, T. M. 1978. A predation model of zooplankton community structure. Verh. Internat. Verein. Limnol. 20: 2496-2500.
- Zaret, T. M. and R. T. Paine. 1973. Species introduction in a tropical lake. Science 182: 449-455. [Cichla ocellares introduced into Gatun Lake Panama and prey diversity declined]
- Zaret, T. M. and W. C. Kerfoot. 1975. Fish predation on Bosmina longirostris: visibility selection versus body-size selection. Ecology 56: 232-237.
- Zaret, T. M. and J. S. Suffern. 1976. Vertical migration as a predator avoidance mechanism. Limnol. Oceanogr. 21: 804-813. [4]

HOW ZOOPLANKTON PREDATORS, ESPCIALLY CALANOIDS, DETECT & INGEST PREY

- Bonnet, D., J Titelman, and R. Harris 2004. *Calanus* the cannibal. J. Plankton Res. 26: 937-948. ["Recent modelling efforts have suggested that cannibalism on eggs and young nauplii is an important factor controlling the population dynamics of Calanus. We measured cannibalistic feeding rates on eggs and nauplii of <u>Calanus helgolandicus</u> in the laboratory."]
- Bundy, M. H., and H. A. Vanderploeg. 2002. Detection and capture of inert particles by calanoid copepods: the role of the feeding current J. Plankton Res. 24: 215-223. ["We document the first observations showing a freely swimming calanoid copepod, <u>Skistodiaptomus</u> <u>oregonensis</u>, attacking prey-sized, non-motile, inert particles entrained in the feeding current before the particles contact the copepod's sensory appendages.... The results of this study show how copepod swimming behaviour, coupled with a low-velocity feeding current, not

only increases copepod encounter rates with inert prey by increasing direct contact rates, but also increases the probability of detecting and capturing remotely located prey that have well-developed escape responses."]

Caparroy, P., Uffe Høgsbro Thygesen, and André W. Visser 2000. Modelling the attack success of planktonic predators: patterns and mechanisms of prey size selectivity. J. Plankton Res. 22: 1871. ["We examine food size spectra of (i) a rheotactic cruising predator, (ii) a suspension-feeding hovering copepod and (iii) a larval fish. For rheotactic predators such as carnivorous copepods, a central assumption of the model is that attack is triggered by prey escape reaction, which in turn depends on the deformation rate of the fluid created by the predator. The model demonstrates that within a species of copepod prey, the ability of larger stages to react at a greater distance from the predator results in increased strike distance and, hence, lower capture probability. For hovering copepods, the vorticity field associated with the feeding current also acts in modifying the prey escape direction."]

Fields, D. M. and J. Yen. 2002. Fluid mechanosensory stimulation of behaviour from a planktonic marine copepod, Euchaeta rimana Bradford J. Plankton Res. 24: 747-755. ["Using a novel technique to create near-field fluid disturbances, we directed microlitre volumes of water towards the antennulary setae. In response to an increasing strength of this purely mechanical signal, the animal varied its behaviour from a rapid flick to a capture response and finally an escape reaction. This work provides a basis for addressing the criteria copepods use to interpret biologically generated signals to elicit an appropriate behavioural response and offers insight into how these signals are differentiated from the random fluid motion in their environment."]

- Greene, C. H. 1986. Patterns of prey selection: implications of predator foraging tactics. Amer. Natur. 128: 824-839.
- Greene, C. H. 1988. Foraging tactics and prey-selection patterns of omnivorous and carnivorous calanoid copepods. Hydrobiologia *167/168*: 295-302.
- Greene, C. H. and M. R. Landry. 1985. Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata* Ecology 66: 1408-1416. [Lab experiments & videotape show that the



intermediate sized Calanus are most vulnerable, and adult sizes of Pseudocalanus. See Yen (1982)] {6}

- Jiang, H., T. R. Osborn, and Charles Meneveau. 2002. Hydrodynamic interaction between two copepods: a numerical study. J. Plankton Res. 24: 235-253. ["Two beneficial roles of the hydrodynamic interactions are suggested for copepod swarms: (1) to maintain the integrity of the swarms and (2) to separate the swarming members with large nearest neighbour distances (usually more than five body lengths). To prevent strong hydrodynamic interactions, copepods in swarms have to avoid positions of strong interactions, such as those directly above or below their neighbours. The results of the velocity magnitudes and deformation rates demonstrate that the hydrodynamic interaction between two copepods generates the hydrodynamic signals detectable by the setae on each copepod's antennules. Based on the threshold of Yen et al. (1992), the results show that the detection distance between two copepods of comparable size is about two to five body lengths."]
- Paffenhöfer, G.-A. and M. G. Mazzocchi. 2002. On some aspects of the behaviour of *Oithona plumifera* (Copepoda: Cyclopoida) J. Plankton Res. 24: 129-135. [Detect prey by mechanoreception]
- Rakusa-Suszczewski, S. 1969. The food and feeding habits of chaetognaths in the seas around the British Isles. Pol. Arch. Hydrobiol. 16: 213-232. [Copepods are the main prey items of the arrow worm, <u>Sagitta</u>. An individual <u>Sagitta</u> can't eat the full array of copepod sizes present. Larger <u>Sagitta</u> eat larger copepods. Guts of each <u>Sagitta</u> contain only a single copepod]

- Saito, H. and T Kiørboe. 2001. Feeding rates in the chaetognath Sagitta elegans: effects of prev size, prey swimming behaviour and small-scale turbulence. J. Plankton Res. 23: 1385-1398.["The gut contents of Sagitta elegans were sampled twice daily (noon and midnight) during 9 days in October at an anchor station in the northern North Sea. ... The average number of prey per chaetognath was among the highest ever recorded, 0.57 ± 0.10 . *Total gut content was independent of ambient* prey concentration, suggesting that feeding rate was saturated. ...copepod males were cleared at rates up to an order of magnitude higher than similarly sized females, probably owing to differences in swimming behaviour. Sagitta elegans is an ambush predator that perceives its prey by hydromechanical signals. Faster swimming prey generates stronger signals and is, hence, perceived at longer distances... It is, therefore, suggested that <u>S. elegans</u> is able to separate prey signals from turbulence signals due to their different spatial characteristics."]
- Svensen, C. and T. Kiørboe. 2000. Remote prey detection in Oithona similis: hydromechanical versus chemical cues. J. Plankton Res. 22: 1155-1166. ["...prey encounter rates and prey reaction distances in the ambush-feeding cyclopoid copepod Oithona similis by video recording freely swimming copepods at different concentrations of prey, the dinoflagellate Gymnodinium dominans. Prey encounter rate increased with prey concentration...prev reaction distance was consistent with that estimated from a ... model of hydromechanical prey perception. ... Our observations are thus inconsistent with remote chemodetection in O.similis. ... ambush-feeding copepods, unlike cruisers and suspension feeders, cannot utilize chemical signals for the detection of individual prev, but rely on either hydromechanical detection or direct interception of prey."]
- Yen, J. 1982. Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. Journal of Experimental Marine Biology and Ecology 63: 105-117. [Lab studies of predation on Dabob Bay calanoid copepods, especially <u>Psudocalanus</u>] [6]
- Yen, J. 1983. Effects of prey concentration, prey size, predator life stage, predator starvation, and seasons on predation rates of the carnivorous copepod *Euchaeta elongata*. Marine Biology 75: 69-77.



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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 and spatial feeding patterns. Limnol. Oceanogr.: 577-597.
- Yen, J. 1988. Directionality and swimming speed in predator-prey and male-female interactions of *Euchaeta rimana*, a subtropical mairne copepod. Bull. Mar. Sci. 43: 395-403.
- Yen, J. and J. R. Strickler. 1996. Advertisement and concealment in the plankton: what makes a copepod hydrodynamically conspicuous. Invertebrate Biology 115: 191-205.

KAIROMONES, VERTICAL MIGRATION & PREDATOR DEFENSE

- Agrawal, A. A., C. Laforsch & R. Tolrian. 1999. Transgenerational induction of defenses in animals and plants. Nature 401: 60-63. [See commentary by Haukioja 1999] *(8, 25)*
- Baumgartner, D., U, Koch and K. O. Rathhaupt. 2003.Alteration of kairomone-induced antipredator response of the freshwater amphipod Gammarus roeseli by sediment type. J Chem Ecol. 29(6):1391-401. [Amphipods switch habitat preference in response to kairomones: "G. roeseli preferred coarse substrates; the highest preference was shown for the most coarse sediment. In the presence of kairomones, the amphipods preferred the less-coarse substrate pebbles over gravel. This difference is an effective antipredator response; <u>G. roeseli</u> is able to hide efficiently in the interstices of the pebbles."]
- Beaton, M. J. and P. D. N. Hebert 1997. The cellular basis of divergent head morphologies in *Daphnia*. Limnol. Oceanogr. 42: 346-356. [?]

Black, A. R. 1993. Predator-induced phenotypic plasticity in *Daphnia pulex*: Life history and morphological responses to *Notonecta* and *Chaoborus*. Limnol. Oceanogr. 38: 986-996. [A variety of behaviors and morphologies induced in lab studies by kairomones from the water strider and phantom midge larvae, including rapid increases in body size and, surprisingly, big-bang reproduction]

- Boersma M., P. Spaak, and L. De Meester. 1998. Predator-mediated plasticity in morphology, life history, and behavior of *Daphnia*: the uncoupling of responses. Amer. Natur. 152: 237-248. [A variety of traits followed in 12 clones from lakes with and without fish. The clones from lakes with fish showed more induction of prey defense behaviors and morphologies, but there was considerable genetic variation.]
- Boersma M., L. De Meester, and P. Spaak. 1999.
 Environmental stress and local adaptation in Daphnia magna. Limnol. Oceanogr. 44: 393-402. [16 clones from lakes with and without fish studied and modeled. Adaptations to fish increase fitness only in lakes with fish relative to the phenotype in the absence of fish.]
- Cousyn C, De Meester L, Colbourne JK, Brendonck L, Verschuren D, Volckaert F. 2001. Proc. Natl. Acad. Sci. USA 98: 6256-6260. ["The population studied experienced variable and well documented levels of fish predation over the past 30 years and shows correlated genetic changes in phototactic behavior, a predator-avoidance trait that is related to diel vertical migration. The changes mainly involve an increased plasticity response upon exposure to predator kairomone, the direction of the changes being in agreement with the hypothesis of adaptive evolution. Genetic differentiation through time was an order of magnitude higher for the studied behavioral trait than for neutral markers (DNA microsatellites), providing strong evidence that natural selection was the driving force behind the observed, rapid, evolutionary changes."]
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- Gool, E. V. and J. Ringelberg. 2002. Relationship between fish kairomone concentration in a lake and phototactic swimming by Daphnia. J. Plankton Res. 24: 713-721. [" It was shown that water from the epilimnion layer increasingly enhanced light-induced swimming reactions until the second week of June, then the effect gradually disappeared. Water from the hypolimnion had no such effect. In 1998, these changes in signal strength correlated with the relative biomass of the 0+ perch, but in 1999, the maximum of the enhancement lagged 2 weeks behind the maximum of the biomass of the 0+ perch. This lag may be due to a different development of the thermocline. We conclude that kairomone concentration may well *correlate with* 0+ *perch biomass and thereby* might inform Daphnia not only about the presence, but also about the abundance, of juvenile perch."]{?}

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- Hessen, D.O. & E. Van Donk, 1993. Morphological changes in *Scenedesmus* induced by substances released from Daphnia. Archiv für Hydrobiologie, *127*: 129-140.
- Hülsmann, S, J. Vijverberg, M Boersmal and W. M. Mooij. 2004.Effects of infochemicals released by gape-limited fish on life history traits of Daphnia: a maladaptive response? Journal of Plankton Research 26: 535-543. ["Life history shifts in daphnids in response to fish infochemicals are generally interpreted as an adaptive response to positive size-selective predation. This interpretation does, however, not hold for larval and small juvenile planktivorous fish, which due to gape limitation, feed on small and medium sized prey. In a life table experiment we show that daphnids exposed to infochemicals excreted by small gape-limited perch and larger perch changed their life history in the same direction, irrespective of the contrasting size-selection of the fish. However, responses to fish infochemicals were strongly influenced by food conditions for daphnids.... Under low food conditions, size at maturity was generally smaller compared with the high food situation, but unaffected by fish infochemicals. By contrast, age at maturity, which was increased at low food levels, was significantly lower in fish treatments compared with the control. We conclude that life history responses of daphnids to gape-limited fish can indeed be maladaptive. but only in situations of high food availability."]
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 23(5):1311-1316. ["These results suggest that metal inhibition of neck tooth induction probably occurs along the signal transduction pathway. Impairment of chemosensory response to predatory chemical cues may have widespread ecological consequences in aquatic systems contaminated by metals."]



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- Rose, R. M., M. St. J. Warne, and R. P. Lim. 2001. Factors Associated with Fish Modify Life History Traits of the Cladoceran Ceriodaphnia cf. dubia J. Plankton Res. 23: 11-17.["A significant (P < 0.05) increase in the mean generation length occurred at a fish density of 16.7 l fish-1. Fish densities of at least 5.9 l fish–1 had a significant (P < 0.05) positive effect on mean brood sizes, population growth rate and net reproductive rate. Increased fish density appeared to increase the length of time during which the cladocerans reproduced significantly (P < 0.05). None of the tested fish densities affected (P > 0.05) cladoceran survival. The observed effects are ascribed to the presence of unidentified substances in the water that previously contained fish. These substances are thought to be 'fish kairomones'."]{}
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- Van gool E, Ringelberg J.1998. Light-induced migration behaviour of *Daphnia* modified by food and predator kairomones. Anim Behav. 1998 Sep;56(3):741-747 ["We studied downward swimming of D. galeataxhyalina in response to stepwise accelerations of relative increases in the intensity of light at several food and fish kairomone concentrations. Both had a modifying, additive, although independent effect."]
- Von Elert, E. & G. Pohnert, 2000. Predator specificity of kairomones in diel vertical migration of Daphnia: a chemical approach. Oikos, 88: 119-128.



- Weber, A. and S. Declerck. 2001. Phenotypic plasticity of Daphnia life history traits in response to predator kairomones: genetic variability and evolutionary potential, Hydrobiologia 360: 89-99.["In a life-table experiment, seven clones of a natural D. galeata population were subjected to kairomones from fish (Perca), from an invertebrate predator (Chaoborus) or a mixture of both. Life history traits were affected by the kairomones of both predators, but effects of Chaoborus were neutralised by Perca in the kairomone mix. No apparent trade-off was found between growth- and reproduction related traits: although daphnids from the Chaoborus treatment grew faster than daphnids from the other treatments, no reduction in the *reproductive output was observed"*]
- Weber, A. and A Van Noordwijk. 2002. Swimming behaviour of Daphnia clones: differentiation through predator infochemicals. J. Plankton Res. 24: 1335-1348. [Variation in small-scale swimming behavior (SSB) in 4 clones of Daphnia galeata in response to predator infochemicals. All of the three tested behavioral parameters (swimming speed, trajectory length and vertical distribution) were affected by the presence of the Chaoborus infochemical, and swimming speed and vertical distribution were also affected by the presence of Perca infochemical. ... The outcome of the predation trial confirms that a decrease in activity is a main factor in lowering Daphnia vulnerability to Chaoborus predation."]
- Weber, A. 2003. More than one `fish kairomone'? Perch and stickleback kairomones affect *Daphnia* life history traits differently, Hydrobiologia 498: 143-150.["Life history traits of <u>Daphnia</u> galeata clones were affected differently by kairomones exuded by two species of fish. The exposure to <u>Gasterosteus</u> kairomone resulted in an increase in population intrinsic rate of increase and body growth rate relative to the exposure to <u>Perca</u> kairomone. ...This raises the possibility that kairomones are cocktails of chemicals rather than a single `fish substance'"]

DORMANCY & DIAPAUSE

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GELATINOUS ZOOPLANKTON

- Chandy, S. T. and C. H. Greene. 1995. Estimating the predatory impact of gelatinous zooplankton. Limnol. Oceanogr. 40: 947-955. [Ctenophore gut contents analyzed and predation rate on copepods estimated]
- Finenko, G. A., Z. A. Romanova, G. I. Abolmasova, B. E. Anninsky, L. S. Svetlichny, E. S. Hubareva, L. Bat, and A. E. Kideys. 2003. Population dynamics, ingestion, growth and reproduction rates of the invader Beroe ovata and its impact on plankton community in Sevastopol Bay, the Black Sea J. Plankton Res. 25: 539-549 ["The impact of the introduced ctenophore Beroe ovata on its prey <u>Mnemiopsis</u> leidyi, another invader ctenophore voraciously feeding on mesozooplankton, and consequently on the mesozooplankton community, was evaluated by undertaking both laboratory and field studies in the northern Black Sea....he B. ovata bloom during the peak M. leidyi biomass resulted in the M. leidyi biomass falling sharply to extremely low values. The predatory impact of M. leidyi on prey zooplankton was found to be reduced during the period of study compared with before. "] {9}
- Greene, C. H., M. R. Landry and B. C. Monger. 1986. Foraging behavior and prey selection by the ambush entangling predator *Pleurobranchia* bachei. Ecology 67: 1493-1501. [Lab studies showed a bimodal selectivity on Calanus in the lab with a reduction in predation on the 1st copepodid Calanus. Acartia and Pseudocalanus were especially vulnerable. Copepod swimming speed is positively correlated with ingestion, with the NVI to CI stage being a slow swimmer] [?]
- Kideys, A. E. 2002. Fall and rise of the Black Sea Ecosystem. Science 297: 1482-1484. [<u>Mnemiopsis</u> was destroying the pelagic community of the Black Sea until Beröe, another ctenophore became abundant] {9}
- Purcell J., J. R. White, M. R. Roman 1994. Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay Limnol. Oceanogr. 39: 263-278. [Neither gelatinous



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zooplankton predation nor food limitation limit Acartia populations in the Bay; other predators perhaps]

- Sullivan, L. J. and D. J. Gifford 2004. Diet of the larval ctenophore Mnemiopsis leidyi A. Agassiz (Ctenophora, Lobata) J. Plankton Res. 26: 417-431. ["Larvae and post-larvae of the lobate ctenophore <u>Mnemiopsis leidyi</u> consumed significant quantities of microphytoplankton and microzooplankton prey... All size classes of <u>M. leidyi</u> larvae and post-larvae derived more nutrition from dinoflagellates than from ciliates. ...The results contradict the prevailing view that all life history stages of <u>M. leidyi</u> are primarily carnivorous."]
- Waggett, R, and J.H. Costello. 1999. Capture mechanisms used by the lobate ctenophore, *Mnemiopsis* leidyi, preying on the copepod Acartia tonsa J. Plankton Res. 21: 2037-2052. ["We recorded interactions between free-swimming M.leidyi and two stages (nauplii, adults) of the calanoid copepod Acartia tonsa.... Prey encounter with <u>Mnemiopsis</u> involved two different processes. The first depended on fluid motions created by the nearly continuous beating of cilia lining the four auricles. These cilia created a low-velocity flow in which A. tonsa nauplii were entrained (94% of naupliar encounters) ... The nauplii, although capable of rapid escape responses, generally appeared to be insensitive to the current in which they were carried. The second process relied upon the collision of swimming prey with the inner surfaces of the oral lobes and was not obviously influenced by the auricular feeding currents. Adult A. tonsa were rarely entrained in the auricular flow, but, instead, propelled themselves into contact with the oral lobes (97% of adult encounters)."]

COMPETITION AMONG ZOOPLANKTON

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Bengtssen J (1987a) Competitive dominance among cladocera: Are single-factor explanations enough? An examination of the experimental evidence. Hydrobiologia 145: 245-257. [Reviews experimental evidence for and against the size-efficiency hypothesis argument that large zooplankton are superior exploitative competitors. Large zooplankton were superior competitors in 18 of 30 tests (and 8 of 10 field experiments)] [4]

- Bengtssen J (1987b) Smaller zooplankton are not superior in exploitative competition: a comment on Persson. Amer. Natur. 129: 928-931. [A comment on a paper arguing that small species were superior. Reviewing his own work, Bengtssen argues that size is not a good predictor of competitive ability]. [4]
- Bengtssen J (1989) Interspecific competition increases local extinction rate in a metapopulation system. Nature 340: 713-715. [Artificial rock pools and zooplankton]
- Borass ME, Seale DB, Horton JB (1990) Resource competition between two rotifer species (*Brachionus rubens* and *B. cayciflours*): an experimental test of a mecahnistic model. J. Plankton Res. 12: 77-87
- Bysstrom P, Persson L, Wahlstrom E (1998) Competing predators and prey: juvenile bottlenecks in whole-lake experiments. Ecology 79: 2153-2167 [A prey fish can reduce the population growth of the juvenile stage of its predator, another fish]
- DeMott WR, Kerfoot WC (1982) Competition among cladocerans: nature of the interaction among Bosmina and Daphnia Ecology 63: 1949-1966 [Dapnhia can suppress but not exclude Bosmina, which can also feed on flagellates]
- Frank PW (1952) A laboratory study of intraspecies and interspecies competition in *Daphnia plicuria* and *Simocephalus velulus*. Physiol. Zool. 25: 178-204
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- Gilbert JJ (1988) Suppression of rotifer populations by Daphnia: a review of the evidence, the mechanisms, and the effects on zooplankton communities. Limnol. Oceanogr. 33: 1286-1303



- Gilbert JJ, MacIsaac HJ (1989) The susceptibility of *Keratella cochlearis* to interference from small cladocerans. Freshwater Biology 32: 333-339
- Hanski I, Ranta E (1983) Coexistence in a patchy environment: three species of *Daphnia* in rock pools. J. Animal Ecology 52: 263-279. [The largest species is the best colonizer but the worst competitor.]
- Harris GP (1986) Phytoplankton ecology: structure, function and fluctuation. Chapman and Hall, London [Competition is discussed on pp. 107-111. The steady-state conditions required by Tilman's model [20-50 d] may not persist long enough for competitive exclusion to occur in nature. On p227 GPH argues <u>a la</u> Andrewartha & Birch (1954) that competition occurs among phytoplankton bur rarely in Nature]
- Hu SS, Tessier AJ (1995) Seasonal succession and the strength of intra- and interspecific competition in a *Daphnia* assemblage. Ecology 76: 2278-2294. [D. galeata replaced D. pulicaria seasonally due to both interspecific and intraspecific competition]
- Lynch M (1977) Zooplankton competition and plankton community structure. Limnol. Oceanogr. 22: 775-777. [Briefly reviews whether food is limiting zooplankton]
- Lynch M (1978) Complex interactions between natural coexploiters - *Daphnia* and *Ceriodaphnia*. Ecology 59: 552-564 [Bottlenecks and facilitation]
- MacIsaac KJ, Gilbert JJ (1989) Competition between rotifers and cladocerans of different body sizes. Oecologia 81: 295-301
- Matveev VF (1987) Effect of competition on the demography of planktonic cladocerans -*Daphnia* and *Diaphanosoma*. Oecologia 74: 468-477
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- Neill WE (1975a) Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826 [Intense competition among cladocera is documented; particularly striking is the competitive exclusion of large <u>Daphnia</u> by the much smaller <u>Ceriodaphnia</u>. Only the juvenile stages of <u>Daphnia</u> are in competition with Ceriodaphnia.]
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- Neill WE (1981) Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. Oecologia 48: 164-177 [When food is abundant, cladoceran densities outstrip control by predators and competition is evident]
- Persson L (1985) Asymmetrical competition: are larger animals competively superior? Amer. Natur. 126: 261-266 [Criticized by Bengtsson]
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- Sale P (1984) The structure of communities of fish on coral reefs and the merit of a hypothesis-testing manipulative approach to ecology. Pp 478-490 *in* Strong DR, Simberloff D, Abele LG and Thistle AB, *eds.* Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton

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intraspecific competition for time or energy: some simple representations. Theor. Pop. Biol. 4: 56-84 [This paper includes a reanalysis of Smith's (1963) <u>Daphnia magna</u> data]

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