ROBERT PTACNIK

Omnivory – the Strategy of Eating your Competitor

Definition of omnivory

In a wider sense, omnivory means the feeding of an organism on several trophic levels. E.g., many birds feed on seeds and fruits (lowest trophic levels) as well as on small animals.

A special case of omnivory is intra-guild predation (IGP, Holt and Polis, 1997). Here the terminal consumer feeds on another heterotrophic consumer, and on the prey of this consumer (see Fig. 1). As a consequence the so-called intermediate consumer suffers from competition for food with the terminal consumer, as well as being prey to the terminal consumer.

Research Fellow Robert Ptacnik,
IFM-GEOMAR,
University of Kiel, Germany.
CAS Fellow 2003/04.

Given the obvious disadvantage for the intermediate consumer, IGP was assumed to be an exception in nature, leading to the extinction of the intermediate consumer sooner or later. This assumption was confirmed by mathematical models showing destabilizing effects of omnivory in simple food web models. This 'finding' supported the view of natural food webs as linear chains, which prevailed in ecology until the early 1980s (e.g. Pimm, 1982). As methods of food-web analysis became more efficient, it became obvious that natural food webs are non-linear, interwoven networks. At the same time, omnivory and IGP were found to be widespread in terrestrial as well as in aquatic food webs.

Modelling helped to find conditions for coexistence of intermediate competitors and their prey. A major prerequisite is that the terminal consumer benefits substantially from the intermediate competitor (Diehl, 2003). In this situation, a strong decline of the intermediate consumer is to the disadvantage of the omnivore, promoting the coexistence of both consumers.

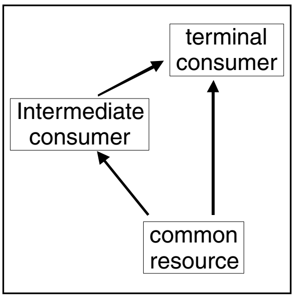

Fig.1. Scheme of intra-guild predation. The intermediate consumer suffers from both competition and predation by the terminal consumer.

Food quality of different trophic levels

The elemental composition of plant and animal biomass varies considerably, with the major differences in the carbon (C) : nitrogen (N) and carbon : phosphorus (P) ratios. Plants are characterized by high C:N and C:P, whereas animals are characterized by low C:N and C:P ratios. This is because carbon is the major component of structural material (cellulose, lignin) in plants. As a result, the food of herbivores (animals feeding on plants) has a much higher C:(N, P) ratio than their own biomass, making especially P and N the growth-limiting nutrients in the food of herbivores. On the other hand, carnivores feed on prey with an elemental composition similar to their own biomass. Because the organic carbon in the prey is not only used for assimilation of biomass, but also as a source of energy, a considerable part of the carbon will be respired, making carbon the limiting nutrient in purely carnivorous organisms.

This difference in the elemental composition of animals and plants is clear-cut in terrestrial ecosystems. In the open-water areas of aquatic ecosystems, 'plants' are represented by unicellular algae (phytoplankton). Being very small and unicellular, these organisms have only minor requirements for structural material, and thus have lower C:(N, P) ratios than plants. As a result, their consumers (zooplankton) can be limited either by mineral nutrients (P, N) or by organic carbon of their prey, depending on the prey species and its physiological state.

In addition to limitation by 'macronutrients' (C, N, P), more complex biochemical compounds can represent a limiting factor in the prey of consumers. Especially some polyunsaturated fatty acids (PUFAs) and amino acids cannot be synthesized by many heterotrophic organisms, but must be consumed with their food. Such biochemical compounds are found in low concentrations in many plant species (incl. some phytoplankton), but not in animals.

Given the nutritional differences between vegetable and animal prey, it is not surprising that some primarily herbivorous organisms enrich their diets by ingesting other heterotrophs.

The example of calanoid copepods

Calanoid copepods are tiny crustaceans (0.5-2 mm in size; related to crabs and crayfish), that live in the open-water zone of lakes and seas. They represent the major trophic link between unicellular organisms (incl. phytoplankton) and planktivorous fish in most marine and in some freshwater ecosystems. While they were originally believed to be herbivorous, research in the last decade has revealed that heterotrophic protists comprise a considerable part of their diet. These heterotrophic organisms constitute high-quality food for the copepods with a high content of nitrogen, phosphorus (low C:(N,P) ratio) and biochemical compounds.

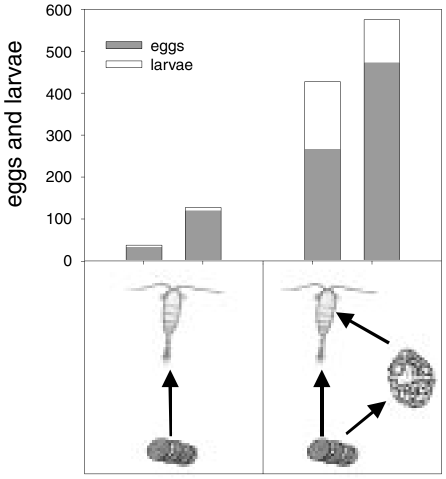

Fig. 2. Cumulative sum of eggs and larvae produced by each of two groups of copepods that were fed either on a pure phytoplankton diet (left side), or on a mixed diet with a protist as intermediate consumers (right side). Phytoplankton was represented by a diatom, *Skeletonema costatum*, the protist by a heterotrophic dinoflagellate, *Gyrodinium sp.* (Ptacnik 2003).

In a simple experiment, copepods were either fed on a pure phytoplankton diet, or on a mixed diet of phytoplankton and a protist, that was itself feeding on the phytoplankton (intermediate consumer, compare with Fig. 1). The reproductive success (eggs and larvae after 6 days of incubation) is displayed in Fig. 2. The obvious difference in reproductive success of the copepods in this experiment was most likely a result of a higher concentration of PUFAs in the heterotrophic protists compared to the phytoplankton (Ptacnik, 2003).

Omnivory in humans and our influence on natural food webs

The growing human population obtains its food from almost every ecosystem on earth. Humans are omnivores that need an animal fraction in their diet to obtain well-balanced nutrition. However, by virtue of our having become such a dominant species, our food pattern affects the fate of various ecosystems.

The strong decline in piscivorous (fish-eating) fish in the world's oceans is maybe the most dramatic example of our influence on natural food webs. Industrial fisheries first focused on large, piscivorous fish. As they were reduced to low levels, mesh-sizes of trawlers were reduced and smaller fish are now harvested ('Fishing down the food web', Pauly et al. 1998). As a consequence, industrial fisheries are threatening large predatory fish nowadays in two ways, by direct reduction, and by reduction of their prey (Fig. 3). Today, the stocks of large piscivorous fish in the world's oceans are approximately 10 % compared to pre-industrial levels (Myers and Worm, 2003).

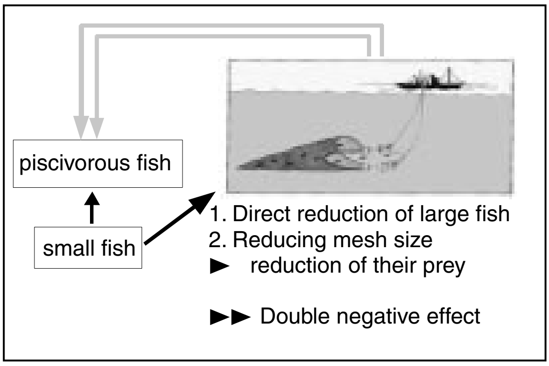

Fig. 3. Direct and indirect negative effects of industrial fisheries on large piscivorous fish.

References

Diehl S. 2003. The evolution and maintenance of omnivory: Dynamic constraints and the role of food quality. *Ecology 84* (10): 2557–2567.

Holt RD, Polis GA. 1997. A theoretical framework for intraguild predation. *Am. Nat.* 149 (4): 745–764.

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F jr. 1998. Fishing Down Marine Food Webs. *Science* 279 (5352): 860–863.

Pimm SL. 1982. *Food Webs*. Chapman & Hall, New York.

Ptacnik, R. 2003. *Omnivory in planktonic food webs: a study on the impact of mixotrophic flagellates and microzooplankton on food web dynamics and productivity*. Dissertation, Institute for Marine Research, Kiel.

Myers RA, Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283.

Thingstad TF, Havskum H, Garde K, et al. 1996. On the strategy of "eating your competitor": A mathematical analysis of algal mixotrophy. *Ecology* 77 (7): 2108–2118.