

MAXIMIZATION VS. COMPENSATION IN STREAM DETRITIVORES: AN APPRAISAL

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It is generally accepted that seasonal fluctuations in the quality of food may influence the life history of a range of aquatic organisms (WHITE, 1978; ANDERSON & CUMMINS, 1979; SWEENEY, 1984; SODERSTROM, 1988). Indeed, increases in the quality of food have been positively correlated to the final size, consumption rates, survivorship, fecundity and growth in many stream invertebrates (ARSUFFI & SUBERKROPP, 1986; SWEENEY *et al.*, 1986; FULLER *et al.*, 1988; GRAÇA, 1990).

Energy budget analyses of animals feeding on different diets enable us to look in more detail at the basis of such physiological responses. Energy budgets relate energy intake to energy expenditure and are comprised of a number of components; consumption (C), defecation (F), absorption ($A=C-F$), respiration (R) and production ($P=A-R$). P, also known as "scope for growth" (SFG), is an indicator of energy available for growth (Pg) and reproduction (Pr),

Assuming no change in R, increases in consumption and absorption will have a positive effect on production. According to the "maximization principle" (Core Neo-Darwinian Hypothesis; CALOW, 1984; 1987), all processes that increase fitness of a species (*e.g.* growth rates, production, etc.) should, by definition, be favored by Natural Selection. Hence, because feeding directly influences growth and reproduction, animals should be operating at maximum rates and efficiencies to use the resources to increase growth, because this will minimize time to maturity and increase their reproductive output. This implies selective feeding on resources that promote better growth.

According to CALOW (1977) and CALOW *et al.* (1981) feeding strategies are also influenced by factors other than food abundance or quality and in the case of species with inflexible life cycles, it is more important that animals keep their development on schedule despite the environmental disturbances and reach particular stages of their development at particular times.

This suggests a compensatory feeding hypothesis which, in contrast to the maximization principle, emphasizes the importance of a "conservative design" aimed at maintaining a cons-

tant *energy intake* "safely tuned" to the mean and variance of the food supply (CALOW, 1975a, b; ROLLO & HAWRYLUK, 1988). According to this hypothesis, ingestion rates should vary inversely with changes in the quality of food.

There is experimental evidence for both, maximization and compensation feeding mechanisms in aquatic invertebrates: examples of higher consumption rates in diets supporting high growth or diets with low C/N ratios include mayflies (SODERSTROM, 1988), the caddisflies *Hesperophylax magnus* and *Psychoglypha sp.* (ARSUFFI & SUBERKROPP, 1986), *Tipula abdominalis* (LAWSON *et al.*, 1984), the snail *Nassarius obsoletus* (PECHENIK & FISHER, 1979) and the stream detritivores *Gammarus pulex* and *Asellus aquaticus* (GRAÇA, 1990). However, other authors reported increases in feeding rates to compensate for decrease in food quality and keep a constant rate of growth in some oligochaetes (MONAKOV, 1972), the amphipods *Gammarus pseudolimnaeus* (BÄRLOCHER & KENDRICK, 1973) the snails *Ancylus fluviatilis*, *Planorbis contortus* (CALOW, 1975a) *Stagnicola elodes* and *Physella gyrina* (ROLLO & HAWRYLUK, 1988).

For stream invertebrates, 3 non-exclusive digestive constraints can possibly be operating and preventing compensation to occur.

(1) If consumption rate is dependent on gut through-put time, then, decreased consumption rate could be a consequence of reduced passage of food through the gut due to low digestibility of structural compounds which constitute a large proportion of unconditioned leaf material. Retaining material in the gut for longer would allow more time for enzymes to work, increasing nutrient extraction and, consequently, the absorption efficiency (CALOW, 1977). In stream detritivores, when feeding on poorly conditioned leaves, it may be more advantageous to further digest material already in the intestine, than ingest new food items. In addition, if nitrogen is low, and locked up in compounds difficult to digest, then, relatively more nitrogen can be extracted from food by slowing down digestion to ensure high degree of enzymatic hydrolysis.

Conditioned leaves have been subjected to the enzymatic activity of fungi and therefore are probably richer in easily digested small-chain polyssacharides. Under these circumstances, a fast gut-passage time strategy might be adopted and consequently it could be more advantageous to ingest "fresh" food, rich in easily digestible compounds, than carry on the enzymatic breakdown of the remaining large-chain polyssacharides.

This view seems to be supported by the observations that the energy content of conditioned food did not change after its passage through the intestine of *G. pulex* and *A. aquaticus* (GRACA, 1990). However, when soaked leaves were offered to the animals, faeces had a significantly lower energy content than the food, suggesting that the animals were extracting more energy per unit of food when feeding on high C/N sources (GRACA, 1990). This also agrees with the observation of NILSSON (1974) that consumption of *G. pulex* feeding on alder, was nearly 10 times higher than on beech, but the capacity of the animals to take energy from beech was higher than from Alder. Again, this was explained by the relatively slow movement of the beech through the gut. Other similar examples are provided by CALOW (1975a,b) and HASSALL & JENNINGS (1975), respectively working with freshwater snails and a terrestrial isopod.

(2) A second explanation for the decrease in consumption rate of animals fed low quality food can be related to the presence of plant allelochemicals. Compounds like polyphenols, tannins, terpenoids and other proteins and saponins are common in long living plants. They have anti-feeding properties, interfering with the available nitrogen, binding to proteins, including digestive enzymes in animal guts, and slowing down digestion (MATTSON, 1980; BERNAYS, 1981). VALIELA *et al.*, (1979) showed that anti-herbivore substances of plant detritus continue to inhibit consumption in detritivores. Freshly fallen leaves are probably richer in these compounds, preventing animals of feeding at higher rates, than older, fully conditioned material. In fact, it has been found that fungi produce several phenol-oxidizing enzymes that probably contribute to the detoxification of phenolic compounds (MARTIN, 1979).

IRONS *et al.*, (1988) offered leaves from 4 species of tree that were submitted to nitrogen and phosphorous enrichment to the caddis *Hydatophylax variabilis*. Leaves were supposedly similar in hardness and microbial conditioning. Larval consumption was positively correlated with nitrogen and negatively correlated with condensed tannin content.

(3) A final explanation for the lack of feeding compensation concerns physical feeding barriers. Conditioned leaves are softer (GRACA, 1990) in comparison with poorly conditioned material. This itself may influence feeding activity. When this ba-

mer was depressed by exposing leaves to hot HCl (BÄRLOCHER & KENDRICK 1975), *Gammarus pseudolimnaeus* preferred leaves treated in this way to control, unconditioned leaves.

Hence, several non-exclusive feeding barriers that might prevent stream detritivores increasing their feeding rates to compensate for low quality food are possible. Their relative importance for aquatic detritivores certainly deserves a deeper examination.

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